
THE SCIENTIFIC MEMOIRS

OF

THOMAS HENRY HUXLEY

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EDITED BY

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THE SCIENTIFIC PAPERS OF THOMAS HENRY HUXLEY

I

ON THE STRUCTURE AND MOTION OF GLACIERS[1]

Philosophical Transactions of the Royal Society, vol. cxlvii., 1857, *pp.* 327–346.
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§ 1.

IN a lecture given at the Royal Institution on the 6th of June, by Mr. Tyndall, 1856, certain views regarding the origin of slaty cleavage were brought forward, and afterwards reported in the 'Proceedings' of the Institution. A short time subsequently, the attention of the lecturer was drawn by Mr. Huxley to the observations of Professor J. D. Forbes on the veined or laminar structure of glacier ice, and the surmise was expressed, that the same explanation might apply to it as to slaty cleavage. On consulting the observations referred to, the probability of the surmise seemed apparent, and the result was a mutual arrangement to visit some of the Swiss glaciers, for the purpose of observing the structure of the ice. This arrangement was carried out, the field of observation comprising the glaciers of Grindelwald, the Aar, and the Rhone. After returning to England, the one in whose department it more immediately lay, followed up the inquiry, which gradually expanded, until at length it touched

[1] The name of Professor John Tyndal, F.R.S., stands with that of Professor Huxley as joint author of this memoir.

the main divisions of the problem of glacier structure and motion. An account of the experiments and observations, and our joint reflections on them, are embodied in the memoir now submitted to the Royal Society.

§ 2. *On the Viscous Theory of Glaciers.*

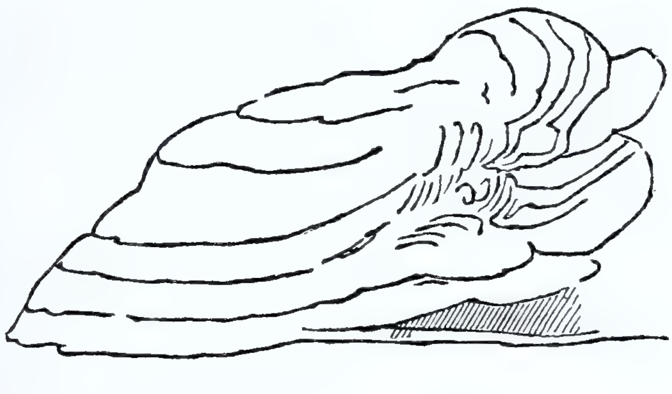
A glacier is a mass of ice which, connected at its upper extremity with the snow which fills vast mountain basins, thrusts its lower extremity into the warm air which lies below the snow-line. The glacier moves. It yields in conformity with the sinuosities of its walls, and otherwise accommodates itself to the inequalities of the valley which it fills. It is not therefore surprising that the glacier should have been regarded as an ice-river by those who dwelt in its vicinity, or that this notion should have found a place in the speculations of writers upon the subject. The statements of M. Rendu in connexion with this point are particularly distinct. "There are," he writes, "a multitude of facts which seem to necessitate the belief that the substance of glaciers enjoys a kind of ductility which permits it to model itself on the locality which it occupies, to become thin and narrow, and to elongate itself like a soft paste."[1] But this observer put forward his speculations with great caution, and often in the form of questions which he confessed his inability to answer. "M. Rendu," says Professor Forbes, "has the candour not to treat his ingenious speculations as leading to any certain result, not being founded on experiments worthy of confidence. . . . . . My theory of glacial motion, then, is this:—A GLACIER IS AN IMPERFECT FLUID OR VISCOUS BODY WHICH IS URGED DOWN SLOPES OF A CERTAIN INCLINATION BY THE MUTUAL PRESSURE OF ITS PARTS."

"The sort of consistency to which we refer," proceeds Professor Forbes, "may be illustrated by that of moderately thick mortar, or the contents of a tar-barrel poured into a sloping channel." Treacle and honey are also referred to as illustrative of the consistency of a glacier. The author of the theory endeavours, with much ability, to show that the notion of semifluidity, as applied to ice, is not an absurdity, but on the contrary, that the motion of a glacier exactly resembles that of a viscous body. Like the latter, he urges, it accommodates itself to the twistings of valleys, and moves through narrow gorges. Like a viscous mass, it moves quickest at its centre, the body there being most free from the retarding influence of the lateral walls. He refers to the "Dirt-Bands" upon the surface of the glacier, and shows that they resemble what would be formed on the

[1] Théorie des Glaciers de la Savoie, p. 84.

surface of a sluggish river. In short, the analogies are put forth so clearly, so ably, and so persistently, that it is not surprising that this theory stands at present without a competitor. The phenomena, indeed, are really such as to render it difficult to abstain from forming some such opinion as to their cause. The resemblance of many glaciers to "a pail of thickish mortar poured out;" the gradual changing of a straight line transverse to the glacier into a curve, in consequence of the swifter motion of the centre; the bent grooves upon the surface; the disposition of the dirt; the contortions of the ice, a specimen of which, as sketched near the Heisseplatte upon the Lower Grindelwald glacier, is given in fig. 1, and of which other striking examples have been adduced by M. Escher, in proof of the plasticity of the substance,—are all calculated to establish the conviction, that the mass must be either viscous, *or endowed with some other*

Fig. 1



property mechanically equivalent to viscosity. The question then occurs, is the viscosity real or apparent? Does any property equivalent to viscosity exist, in virtue of which ice can move and mould itself in the manner indicated, and which is still in harmony with our experience of the non-viscous character of the substance? If such a property can be shown to exist, the choice will rest between a quality which ice is *proved* to possess, and one which, in opposition to general experience, it is assumed to possess, in accounting for a series of phenomena which either the real or the hypothetical property might be sufficient to produce. In the next section, the existence of a true cause will be pointed out, which reconciles the properties of ice, exhibited even by hand specimens, with the apparent evidences of viscosity already referred to, and which, though it has been overlooked hitherto, must play a part of the highest importance in the phenomena of the glacier world.

§ 3. *On the Regelation of Ice, and its application to Glacial Phenomena.*

In a lecture given by Mr. Faraday at the Royal Institution on the 7th of June, 1850, and briefly reported in the 'Athenæum' and 'Literary Gazette' for the same month, it was shown that when two pieces of ice, at 32° Fahr., with moistened surfaces, were placed in contact, they became cemented together by the freezing of the film of water between them. When the ice was below 32°, and therefore dry, no adhesion took place between the pieces. Mr. Faraday referred, in illustration of this point, to the well-known experiment of making a snowball. In frosty weather the dry particles of ice will scarcely cohere, but when the snow is in a thawing condition, it may be squeezed into a hard compact mass. On one of the warmest days of last July, when the thermometer stood at upwards of 80° Fahr. in the shade and above 100° in the sun, a pile of ice-blocks was observed by one of us in a shop window, and he thought it interesting to examine whether the pieces were united at their places of contact. Laying hold of the topmost block, the whole heap, consisting of several large lumps, was lifted bodily out of its vessel. Even at this high temperature the pieces were frozen together at the places of contact, though the ice all round these places had been melted away, leaving the lumps in some cases united by slender cylinders of the substance. A similar experiment may be made in water as hot as the hands can bear; two pieces of ice will freeze together, and sometimes continue so frozen in the hot water, until, as in the case above mentioned, the melting of the ice around the points of contact leaves the pieces united by slender columns of the substance.

Acquainted with these facts, the thought arose of examining how far, in virtue of the property referred to, the *form* of ice could be changed without final prejudice to its continuity. It was supposed that though crushed by great pressure, new attachments would be formed by the cementing, through regelation, of the severed surfaces; and that a resemblance to an effect due to viscosity might be produced. To test this conjecture the following experiments were made:—Two pieces of seasoned boxwood, A and B, fig. 2, 4 inches square and 2 deep, had two cavities hollowed out, so that when one was placed upon the other, a lenticular space, shown in section at C, was enclosed between them. A *sphere* of compact, transparent ice, of a volume rather more than sufficient to fill the cavity, was placed between the pieces of wood, and subjected to the pressure of a small hydraulic press. The ice broke, as was expected, but it soon

re-attached itself; the pressure was continued, and in a few seconds *the sphere was reduced to a transparent lens of the shape and size of the mould in which it had been formed.*

This lens was placed in a cylindrical cavity, two inches wide and half an inch deep, hollowed out in a piece of boxwood, C, fig. 3, as

Fig. 2.

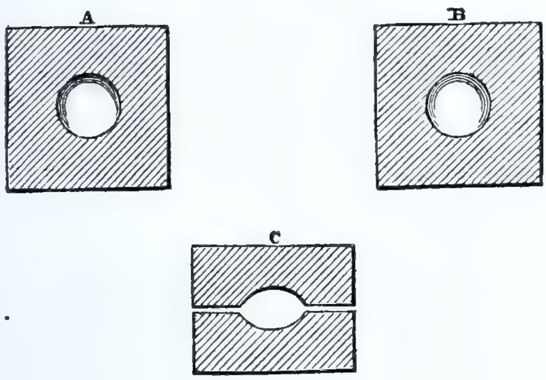
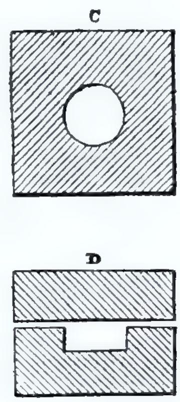


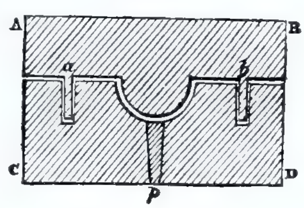
Fig. 3.



before; a *flat* plate, D, of the wood being placed over the lens, it was submitted to pressure. The lens broke as the sphere did, but the fragments attached themselves in accordance with their new conditions, *and in less than half a minute the mass was taken from the mould a transparent cake of ice.*

The substance was subjected to a still severer test. A hemispherical cavity was hollowed out in a block of boxwood, and a protuberant hemisphere was turned upon a second slab of the wood, so that, when the protuberance and the cavity were concentric, a distance of a quarter of an inch separated the convex surface of the former from the concave surface of the latter. Fig. 4 shows the arrangement in section. The pins of brass, *ab*, fixed in the slab AB, and entering suitable apertures in the mould CD, served to keep the two surfaces concentric.

Fig. 4.

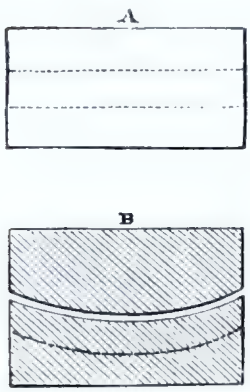


A lump of clear ice was placed in the cavity, the protuberance was brought down upon it, and the mould submitted to hydraulic pressure. After a short interval, it was taken from the press, and when the upper slab was removed, a smooth concave surface of ice was exposed. By tapping the conical plug *p*, this ice was lifted from the cavity, *the lump having been converted by pressure into a hard transparent cup of ice.*

The application of the results here obtained to the "viscous flow" of glaciers, will perhaps be facilitated by the following additional experiments.

A block of boxwood (A, fig. 5), 4 inches long, 3 wide and 3 deep, had its upper surface slightly curved, and a longitudinal groove (shown in dots in the figure), an inch wide and an inch deep, worked into it. A slab of the wood was prepared, the under surface of which was that of a convex cylinder, curved to the same degree as the concave surface of the former piece. The arrangement is shown in section at B. A straight prism of clear ice, 4 inches in length, an inch wide, and a little more than an inch in depth, was placed in the groove, and the upper slab of boxwood was placed upon it. The mould was submitted to hydraulic pressure, as in the former cases; the prism broke as a matter of course, but the quantity of ice being rather more than sufficient to fill the groove, and hence projecting above its edge, the pressure brought the fragments together and re-established the continuity of the ice. After a few seconds it was taken from the mould, bent as if it had been a plastic mass. Three other moulds similar to the last, but of augmenting curvature, were afterwards made use of, the same prism being passed through all of them in succession. *At the conclusion of the experiments the prism came out, bent to a transparent semi-ring of solid ice.*

Fig. 5.



In this way, by the proper application of force, all the bendings and contortions observed in glacier ice, and adduced in proof of its viscosity, can be accurately imitated. Any observer, seeing a straight bar of ice converted into a continuous semi-ring without being aware of the quality referred to, and having his attention fixed on the changes of external form alone, would be naturally led to the conclusion that the substance is viscous. But it is plainly not viscosity, properly so called, which enables it to change its shape in this way, but a property which has hitherto been entirely overlooked by writers upon glaciers.

It has been established by observation, that a vertical layer of ice originally plane, and perpendicular to the axis of a glacier, becomes bent, because the motion of its ends is retarded in comparison with that of its centre. This is the fact upon which the viscous theory principally rests.

In the experiments with the straight prism of ice, four successive

moulds, gradually augmenting in curvature, were made use of. In passing suddenly from the shape of one to that of the other, the ice was fractured, but the pressure brought the separated surfaces again into contact and caused them to freeze together, thus restoring the continuity of the mass. The fracture was in every case both audible and tangible; it could be heard and it could be felt. A series of cracks occurred in succession as the different parts of the ice-prism gave way, and towards the conclusion of the experiment, the crackling in some instances melted into an almost musical tone. But if instead of causing the change to take place by such wide steps as those indicated; if instead of four moulds, forty, or four hundred were made use of; or better still, suppose a single mould to have the power of gradually changing its curvature from a straight line to a semicircle under the hydraulic press; the change in the curvature of the ice would closely approximate to that of a truly plastic or viscous body. This represents the state of things in a glacier. A transverse plate of ice, situated between the mass in front of it and the mass behind, is virtually squeezed in a press of the description which has been just imagined. The curvature of the ice-mould *does* change in the manner indicated, and so slowly, that the bending closely resembles what would take place if the substance were viscous. The gradual nature of the change of curvature may be inferred from an experiment made by Professor Forbes on an apparently compact portion of the Mer de Glace. He divided a distance of 90 feet transverse to the axis of the glacier into spaces of two feet each, and observed with a theodolite the gradual passage of this straight line into a bent one. The row of pins bent gradually so as to form a curve convex towards the lower extremity of the glacier; their deviations from a perfect curve were slight and irregular, nor was any great dislocation to be observed throughout their whole extent. After six days the summit of the curve formed by the forty-five pins was one inch in advance of the straight cord which united its two ends. It is not surprising if, with this extremely gradual change, the motion should have appeared to be the result of viscosity. It may, however, be remarked, that the slight and irregular variations to which Professor Forbes alludes, and which are such as would occur if the motion were such as we suppose it to be, are likely to throw much light upon the problem. It is also extremely probable that the motion, if effected in the manner referred to, will be sometimes accompanied by an audible crackling of the mass. To this we paid but little attention when on the ground; for the significance of this, as well as of many other points, was first suggested by the experiments made after our return. It is, however,

we believe, a phenomenon of common occurrence. Professor Forbes calls the glacier a "crackling mass;" he speaks of the ice "cracking and straining forwards;" and in that concluding passage of his 'Travels' which has excited such general admiration, he says of the glacier, "it yields groaning to its fate." Other observers make use of similar expressions. M. Desor also speaks of the sudden change of the colour of the blue veins of the ice where a portion of the central moraine near the Abschwung is cleared away; the observation is very remarkable. "Au moment," says M. Desor, "où on la met à découvert, la glace des bandes bleues est parfaitement transparente, l'œil y plonge jusqu'à une profondeur de plusieurs pieds, mais cette pureté ne dure qu'un instant, et l'on voit bientôt se former des petites fêlures d'abord superficielles, qui se combinent en réseau de manière à enlever peu à peu à la glace bleue toute sa transparence. Ces fêlures propagent également dans les bandes blanches, et lorsqu'on approche l'oreille de la surface de la glace, en entend distinctement un *léger bruit de crépitation* qui les accompagnent au moment de leur formation." These facts appear to be totally at variance with the idea of viscosity.

In a chapter on the "Appearance of the larger Glaciers," in an interesting little work by M. Mousson of Zürich, for which one of us has to thank the kindness of Professor Clausius, the phenomena which they exhibit are thus described:—[1] "The appearance of a large glacier of the first order has been compared, not without reason, with that of a high swelled, and suddenly solidified stream. It winds itself in a similar manner through the curving of the valley, is deflected by obstacles, contracts its width, or spreads itself out. . . . . . In short, the form is modified in the most complete manner to suit the character and irregularities of its bed. To this capacity to change its form, the ice of glaciers unites another property, which reminds us of the fluid condition; namely, the capability of joining and blending with other ice. Thus we see separate glacier branches perfectly uniting themselves to a single trunk; regenerated glaciers formed from crushed fragments; fissures and chasms closed up, and other similar appearances. These phenomena evidently point to a slow movement of the particles of which the glacier consists; strange as the application of such an idea to a solid brittle mass such as glacier ice may appear to be. The solution of this enigma constitutes one of the most difficult points in the explanation of glaciers."

When the appearances here enumerated are considered with reference to the experiments on the regelation of ice above described,

[1] Die Gletscher des Jetztzeit, by Albert Mousson. Zürich, 1854.

the enigma referred to by the writer appears to have received a satisfactory solution. The glacial valley is a mould through which the ice is pressed by its own gravity, and to which it will accommodate itself, while preserving its general continuity, as the hand specimens do to the moulds made use of in the experiments. Two glacial branches unite to form a single trunk, by the regelation of their pressed surfaces of junction. Crevasses are cemented for the same reason; and the broken ice of a cascade is reconstituted, as a heap of fragments under pressure become consolidated to a single mass. To those who occupy themselves with the external conditions merely of a glacier, it may appear of little consequence whether the flexures exhibited by the ice be the result of viscosity or of the principle demonstrated by the experiments above described. But the natural philosopher, whose vocation it is to inquire into the inner mechanism concerned in the production of the phenomena, will discern in the yielding of a glacier a case of simulated fluidity hitherto unexplained, and perhaps without a parallel in nature.

§ 4. *On the Veined Structure of Glacial Ice.*

This structure has been indifferently called the "veined structure," the "banded structure," the "ribboned structure," and the "laminar structure," of glacial ice. In a communication to the Geological Society of France assembled at Porrentruy in September, 1838, M. Guyot gave the following interesting description of the phenomenon:—"Since the word layer has escaped me, I cannot help recording as a subject of investigation for future observers a fact, regarding which I dare not hazard an explanation; especially as I have not encountered it more than once. It was at the summit of the Gries, at a height of about 7500 feet, a little below the line of the first or high nevé, where the ice passes into a state of granular snow. . . . . . In ascending to the origin of this latter (the glacier of Bettelmatten), for the purpose of examining the formation and direction of the great transverse fissures, I saw under my feet the surface of the glacier entirely covered with regular furrows, from 1 to 2 inches in width, hollowed in a half snowy mass, and separated by protruding plates of an ice more hard and transparent. It was evident that the mass of the glacier was here composed of two sorts of ice, one that of the furrows, still snowy and more easily melted, the other that of the plates, more perfect, crystalline, glassy and resistent; and that it was to the unequal resistance which they presented to the action of the atmosphere that was due the hollowing of the furrows and the

protrusion of the harder plates. After having followed them for several hundred yards, I reached the edge of a great fissure, 20 or 30 feet wide; which cutting the plates and furrows perpendicularly to their direction, and exposing the interior of the glacier to a depth of 30 or 40 feet, permitted the structure to be observed on a beautiful transverse section. As far down as my vision could reach I saw the mass of the glacier composed of a multitude of layers of snowy ice, each two separated by one of the plates of ice of which I have spoken, and forming a whole regularly laminated in the manner of certain calcareous slates."

A description of this structure, as observed upon the glacier of the Aar, was communicated by Professor Forbes to the Royal Society of Edinburgh on the 6th of December, 1841, and published in the Edinburgh New Philosophical Journal for 1842.[1] He was undoubtedly the first to give the phenomenon a theoretic significance.

While engaged in the Lower Grindelwald glacier, we separated plates of ice perpendicular to the lamination of the glacier. The appearance presented on looking through them was that sketched in fig. 6. The layers of transparent ice seemed imbedded in a general milky mass; through the former the light reached the eyes, while it was intercepted by the latter. Some of the transparent portions were sharply defined, and exhibited elongated oval sections, resembling that of a double convex lens, and we therefore called this disposition of the veins "*the lenticular structure*." In other cases, however, the sharpness of outline did not exist, but still the tendency to the lenticular form could be discerned, the veins in some cases terminating in washy streaks of blue. This structure is probably the same as that observed by Professor Forbes on the Glacier des Bossons, and described in the following words:—"The veins and bands . . . . . are not formed in this glacier by a simple alternation of parallel layers, but the icy bands have all the appearance of posterior infiltration, occasioned by fissures, *thinning off both ways*." [2]

Fig. 6.

In 1842 Professor Forbes undertook the survey and examination of the Mer de Glace, and finally arrived at a theory of glacier lamina-

[1] This communication gave rise to a discussion as to priority between Professor Forbes and M. Agassiz, for the details of which we must refer to the original papers on the subject.

[2] Travels, p. 181.

tion, which both in his 'Travels' and in a series of letters, extending over a period of several years, he has expounded and illustrated with great skill. The theory is summed up in the following words:—"The whole phenomena in the case of any of the semifluids I have mentioned (treacle, tar, &c.), are such as, combined with the evidence which I have given, that the motion of a glacier is actually such as I have described that of a viscid fluid to be, can leave, I think, no reasonable doubt, *that the crevices formed by the forced separation of a half rigid mass, whose parts are compelled to move with different velocities, becoming infiltrated with water, and frozen during winter, produce the bands which we have described.*"[1]

This theory has been opposed by Mr. Hopkins, whose excellent papers, published in the 26th volume of the Philosophical Magazine, are replete with instruction as to the mechanical conditions of glaciers. On the other hand, the theory of Professor Forbes is defended in the same journal by Dr. Whewell.[2] We will leave the points discussed in their communications for the present untouched, and confine ourselves to stating a few of the circumstances which appear to us to render the theory doubtful.

1. It is not certain that the colds of winter penetrate to depths sufficient to produce the blue veins, which, it is affirmed, are "an integral part of the inmost structure" of the ice. Saussure was of opinion that the frosts of winter did not penetrate to a greater depth than 10 feet, even at the summit of Mont Blanc, and Professor Forbes considers this opinion to be a just one. But if so, there would be some difficulty in referring to the frosts of winter the blue veins which M. Agassiz observed at a depth of 120 feet below the surface of the glacier of the Aar.

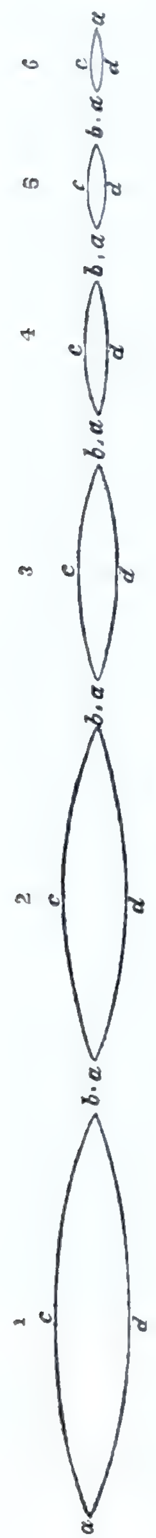
2. It will be remembered that M. Guyot's statement regarding the blue veins is, that he saw the mass of the glacier composed of a multitude of layers of white ice, separated, each from the other, by a plate of transparent ice. The description of Professor Forbes is briefly this:—"Laminæ or thin plates of transparent blue ice alternate in most parts of every glacier with laminæ of ice, not less hard and perfect, but filled with countless air-bubbles which give it a frothy semi-transparent look." But there is another form of the blue

[1] Travels, p. 377. M. Agassiz also seems disposed to regard the blue bands as the result of the freezing up of fissures, which, however, are supposed to be formed in a manner different from that assumed by Professor Forbes. But M. Agassiz calls the attention of future observers to some of the related phenomena; and gives it as his opinion, "qu'il n'est aucune phénomène dont l'explication offre plus des difficultés." See his important work, 'Système Glacière,' which, until quite recently, we had not the opportunity of examining.

[2] Philosophical Magazine, S. 3, vol. xxvi. pp. 171, 217.

veins, already referred to, which consists in transparent lenticular masses imbedded in the general substance of the white ice. Horizontal sections of these transparent lenses were exposed upon the surface of the Grindelwald glacier, and vertical sections of them upon the perpendicular sides of the water-courses, and upon the walls of the crevasses. The accompanying measurements (fig. 7), taken on the spot, will give an idea of their varying dimensions. Such masses as these here figured were distributed in considerable numbers through the glacier; they had all the appearance of flattened cakes, and the smaller ones resembled the elongated green spots exhibited by sections of ordinary roofing-slate cut perpendicular to the planes of cleavage. Now it appears mechanically impossible that a solution of continuity, such as that supposed, could take the form of the detached lenticular spaces above figured.

Fig. 7.



Dimensions.

		in.		in.			in.		in.
No. 1.	*ab*	24	*cd*	2	No. 4.	*ab*	$3\frac{1}{2}$	*cd*	$\frac{1}{2}$
2.	*ab*	10	*cd*	1	5.	*ab*	$1\frac{3}{4}$	*cd*	$\frac{1}{4}$
3.	*ab*	6	*cd*	1	6.	*ab*	1	*cd*	$\frac{1}{12}$

3. The fissures to which the blue veins owe their existence are stated to be due to the motion of the glacier; and as this motion takes place both in summer and winter, it is to be inferred that the fissures are produced at both seasons of the year. Now as the fissures formed in winter cannot be filled with ice during that season for want of *water*, and as those formed in the ensuing summer cannot, while summer continues, be frozen for want of *cold*, we ought at the end of each summer to have *a whole year's fissures* in the ice. These fissures, which the ensuing winter is, according to the theory, to fill with blue ice, must, in summer, be filled with *blue water*. *Why then are they not seen in summer?* The fissures are such as can produce plates of ice varying "from a small frac-

tion of an inch to several inches in thickness," which, according to our own observations, produce lenticular masses of ice 2 feet long and 2 inches thick, or even (for we have seen pieces of this description) 10 feet long and 10 inches thick; and M. Desor informs us in the memoir from which we have already quoted, that under the medial moraine of the Aar glacier, there are bands 10 inches and even a foot in thickness. Such fissures could not escape observation if they existed, but they never have been observed, and hence the theory which makes their pre-existence necessary to the production of the blue veins appears to us improbable.

§ 5. *On the Relation of Slaty Cleavage to the Veined Structure.*

Within the last few years a mechanical theory of the cleavage of slate rocks has been gradually gaining ground among those who have reflected upon the subject. The observations of the late Daniel Sharpe appear to have originated this theory. He found that fossils contained in slate rocks were distorted in a manner which proved that they had suffered compression in a direction at right angles to the planes of cleavage. His specimens of shells, which are preserved in the Museum of Practical Geology, and other compressed fossils in the same collection, illustrate in a remarkable manner his important observations. The subsequent microscopic observations of Mr. Sorby, carried out with so much skill and patience, show convincingly that the effects of compression may be traced to the minutest constituents of the rocks in which cleavage is developed. More recently, Professor Haughton has endeavoured to give numerical accuracy to this theory, by computing, from the amount of the distortion of fossils, the magnitude of the change which cleaved rocks have undergone. By the united testimony of these and other observers, whose researches have been carried out in different places, the association of cleavage and compression has been established in the most unequivocal manner; and hence the question naturally arises, "Is the pressure sufficient to produce the cleavage?" Sharpe appears to have despaired of an experimental answer to this question. "If," says he, "to this conclusion it should be objected, that no similar results can be produced by experiment, I reply, that we have never tried the experiment with a power at all to be compared with that employed; and that this may be one of the many cases where our attempts to imitate the operations of nature fail, owing to the feebleness of our means, and the shortness of the period during which we can employ them." The same opinion appears to have been entertained by Professor Forbes:

—"The experiment," he says, "is one which the boldest philosopher would be puzzled to repeat in his laboratory; it probably requires acres for its scope, and years for its accomplishment."

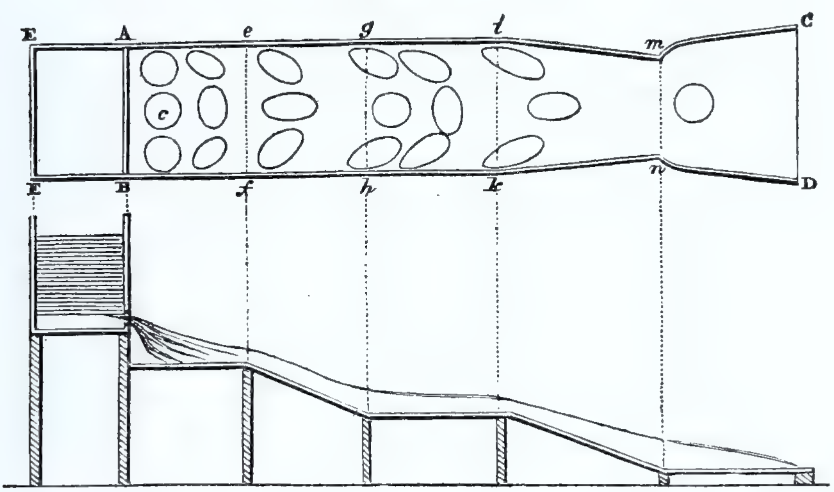
While one of us was engaged in 1855 in examining the influence of pressure upon magnetism, he was fortunate enough to discover that in white wax, and other bodies, a cleavage of surpassing fineness may be developed by pressure, and he afterwards endeavoured, in a short paper,[1] to show the application of this result, both to slaty cleavage and to a number of other apparently unrelated phenomena. The theory propounded in this paper may be thus briefly stated. If a piece of clay, wax, marble or iron be broken, the surface of fracture will not be a plane surface, nor will it be a surface dependent only on the form of the body and the strain to which it has been subjected; the fracture will be composed of innumerable indentations, or small facets, each of which marks a surface of weak cohesion. The body has yielded, where it could yield, most easily, and in exposing these facets, in some cases crystalline, in others purely mechanical, wherever the mass is broken, it is shown to be composed of an aggregate of irregularly-shaped parts, which are separated from each other by surfaces of weak cohesion. Such a quality must, in an eminent degree, have been possessed by the mud of which slate-rocks are composed, after the water with which the mud had at first been saturated had drained away; and the result of the application of pressure to such a mass would be, to develop in it a lamination similar to that so perfectly produced on a small scale in white wax. Thus one cause of cleavage may be stated, in general terms, to be the conversion by pressure of irregularly-formed surfaces of weak cohesion into parallel planes. To produce lamination in a compact body such as wax, it is manifest that while it yields to the compression in one direction, it must have an opportunity of expanding in a direction at right angles to that in which the pressure is exerted; a second cause is the lateral sliding of the particles which thus takes place, and which may be very influential in producing the cleavage.[2]

[1] Proceedings of the Royal Institution, June 1856; Philosophical Magazine for July 1856.

[2] Three principal causes may operate in producing cleavage:—1st, the reducing of surfaces of weak cohesion to parallel planes; 2nd, the flattening of minute cavities; and 3rd, the weakening of cohesion by tangential action. The third action is exemplified by the state of the rails near a station where the break is applied. In this case, while the weight of the train presses vertically, its motion tends to cause longitudinal sliding of the particles of the rail. Tangential action does not however necessarily imply a force of the latter kind. When a solid cylinder, an inch in height, is squeezed by vertical pressure to a cake a quarter of an inch in height, it is impossible, physically speaking, that the particles situated in the same

Before attempting to show the connexion between this theory and the case at present under consideration, a mode of experiment may be described which was found to assist in forming a conception of the mechanical conditions of a glacier, and which has already been resorted to by Professor Forbes in demonstration of the viscous theory. Owing to the property of ice described in § 3, the resemblance between the motion of a substance like mud and that of a glacier is so great, that considerable insight regarding the deportment of the latter may be derived from a study of the former. From the manner in which mud yields when subjected to mechanical strain,

Fig. 8.



we may infer the manner in which ice would be *solicited to yield* under the same circumstances.

To represent then the principal accidents of a glacial valley, a wooden trough, ABCD, fig. 8, of varying width and inclination, was made use of. From A to C the trough measures 6 feet, and from A to B 15 inches. It is divided into five segments; that between AB and *ef* is level, or nearly so, that between *ef* and *gh* is inclined;

vertical line shall move laterally with the same velocity; but if they do not, the cohesion between them will be weakened or ruptured. The pressure will produce new contact, and if the new contact have a cohesive value equal to that of the old, no cleavage from this cause can arise. The relative capacities of different substances for cleavage, appears to depend in a great measure upon their different properties in this respect. In butter, for example, the new attachments are equal, or nearly so, to the old, and the cleavage is consequently indistinct; in wax this does not appear to be the case, and hence may arise in a great degree the perfection of its cleavage. The further examination of this subject promises interesting results.

from *gh* to *ik* is again nearly level; from *ik* to *mn* inclined, while from *mn* to CD the inclination is less than between *ik* and *mn*. The section of the bottom of the trough is figured underneath the plan. ABEF is a box supported at the end of the trough, and filled with a mixture of water and fine pipe-clay. The front, AB, can be raised, like a sluice, and the mud permitted to flow regularly into the trough. While the mud is in slow motion, a coloured circle, *c*, is stamped upon the white clay between AB and *ef*; the changes of shape which this circle undergoes in its passage downwards will indicate the forces acting upon it. The circle first moves on, being rather compressed, in the direction of the length of the trough until it reaches *ef*, on crossing which, and passing down the subsequent slope, it elongates as in the figure. Between *gh* and *ik* the figure passes through the circular form, and assumes that of an ellipse, whose shorter axis is parallel to the length of the trough. It is manifest from this that the mud between *ef* and *gh* is in a state of longitudinal tension, while between *gh* and *ik* its state is that of longitudinal compression. On crossing *ik* and descending the second incline, the figure is again drawn out longitudinally, while between *mn* and CD the ellipse widens on account of the permission given to lateral expansion by the augmented width of the trough.

The side circles in the same figure will enable us to study the influence of lateral friction upon the descending stream. These circles are distorted into ellipses, whose major axes are oblique to the direction of the trough's length. Above the line *ef* central fissures perpendicular to the axis of the trough cannot be formed; for here, instead of tending to open into fissures, the flattening of the central circle shows that the mud is longitudinally compressed. On the slope below *ef*, the distortion of the circles into ellipses is very pronounced; and as the longer axis of each ellipse marks the line of maximum tension, and as the tendency of the mass is to form a fissure at right angles to such a line, we should have here, if the substance were not so plastic as to prevent the formation of fissures, the state of things observed upon the corresponding portion of the glacier; namely, central fissures perpendicular to the longitudinal axis of the trough, and side fissures inclined to the same axis because pointing in the direction of the shorter axis of each ellipse. Between *gh* and *ik* the longitudinal tension is changed to compression; the central figure is flattened, while the side ones remain stretched. In the corresponding portion of the glacier we should expect the central fissures formed between *ef* and *gh* to be squeezed together and closed up, while the

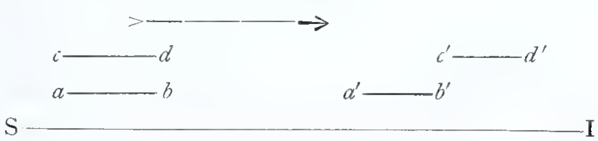
lateral ones would remain open. This is also the case.[1] Between *ik* and *mn* we have again longitudinal tension, and at the corresponding portions of the glacier the transverse central crevasses ought to reappear, which they actually do. Below the line corresponding to *mn*, the widening of the valley, in the case now in our recollection, causes the ridges produced at the previous slope to break across and form prismatic blocks ; while lower down the valley these prisms are converted by the action of sun and rain into shining minarets of ice. These results appear to be in perfect accordance with those arrived at by Mr. Hopkins on strict mechanical reasoning.[2]

We will now seek to show the analogy of slaty cleavage to the laminar structure of glacier ice. Referring to fig. 8, it will be seen that in the distortion of the side circles one diameter is elongated to form the transverse axis of the ellipse, while another is compressed to form the conjugate axis. In a substance like mud, as the elongation of the major axis continues, its inclination to the axis of the glacier continually changes ; but were the substance one of limited extensibility like ice, fissures would be formed when the tension had reached a sufficient amount, or in other words, when the major axis of the ellipse had assumed a definite inclination to the axis of the glacier.

Thus, in a glacier of the form represented by our trough owing to the swifter motion of the centre, we have a line of maximum pressure oblique to the wall of the glacier, and a line of maximum tension perpendicular to the former ; crevasses are formed at right angles to the direction of tension, and *it is approximately at right angles to the direction of pressure, as in the case of slate rocks, that the lamination of glacier ice is developed.*

Under ordinary circumstances, therefore, the lamination near the

[1] The possibility of the coexistence of lateral crevasses and compression at the centre may, perhaps, be thus rendered manifest :—let *ab*, *cd* be two linear elements of a glacier, situated near its side SI.



Suppose, on passing downwards, the line *ab* becomes shortened by longitudinal pressure to *a'b'*, and *cd* to *c'd'*, which latter has passed *a'b'* on account of its greater distance from the side of the glacier. Taking the figure to represent the true change both of dimension and position, it is plain, that though each element has been *compressed*, the differential motion has been such as to *distend* the line of particles joining *a* and *d*, in the ratio $\frac{ad}{a'd'}$. If this ratio be more than that which the extensibility of ice can permit of, a side fissure will be formed.

[2] Philosophical Magazine, 1845, vol. xxvi.

sides of the glacier would, in accordance with the theory of compression, be oblique to the sides, which it actually is. It would be transverse to the crevasses wherever they occur, which it actually is. If the bed of a glacier at any place be so inclined as to cause its central portions to be longitudinally compressed, the lamination, if due to compression, ought to be carried across the glacier at such a place, being transverse to the axis of the glacier at its centre, which is actually the case. This relation of the planes of lamination to the direction of pressure is constant under a great variety of conditions. A local obstacle which produces a thrust and compression is also instrumental in developing the veined structure. In short, so far as our observations reach, wherever the necessary pressure comes into play, the veined structure is developed; being always approximately at right angles to the direction in which the pressure is exerted.

But we will not rely in the present instance upon our own observations alone. Before he formed any theory of the structure, and in his first letter upon the subject, Professor Forbes remarks, that "the whole phenomenon has a good deal the air of a structure induced *perpendicularly to the lines of greatest pressure.*" His later testimony is in substance the same. In his thirteenth letter, read before the Royal Society of Edinburgh on the 2nd of December, 1846, he says that the blue veins are formed *where the pressure is most intense.* In his reference to the development of the laminar structure on the glacier of the Brenva, the pressure is described as being "*violent,*" the effect being such as to produce "*a true cleavage when the ice is broken with a hammer or cut with an axe.*" So also with regard to the glacier of Allalein,[1] he says "the veined structure is especially developed in front, *i.e.* against the opposing side of the valley, where the pressure is greater than laterally." In fact, the parallelism of the phenomenon to that of slaty cleavage struck Professor Forbes himself, as is evident from the use of the term "now" in the following passage:—"It will be understood that I do not *now* suppose that there is any parallelism between the phenomenon of rocky cleavage and the ribboned structure of the ice." This reads like the giving up of a previously held opinion; the term *now* being printed in italics by Professor Forbes himself. The adoption of the viscous theory appears to have carried the renunciation of this idea in its train.

Later still, and from a source wholly independent of the former, we have received additional testimony on the point in question. The following quotation is from a letter, dated 16th November, 1856, received by one of us from Professor Clausius of Zurich, so well

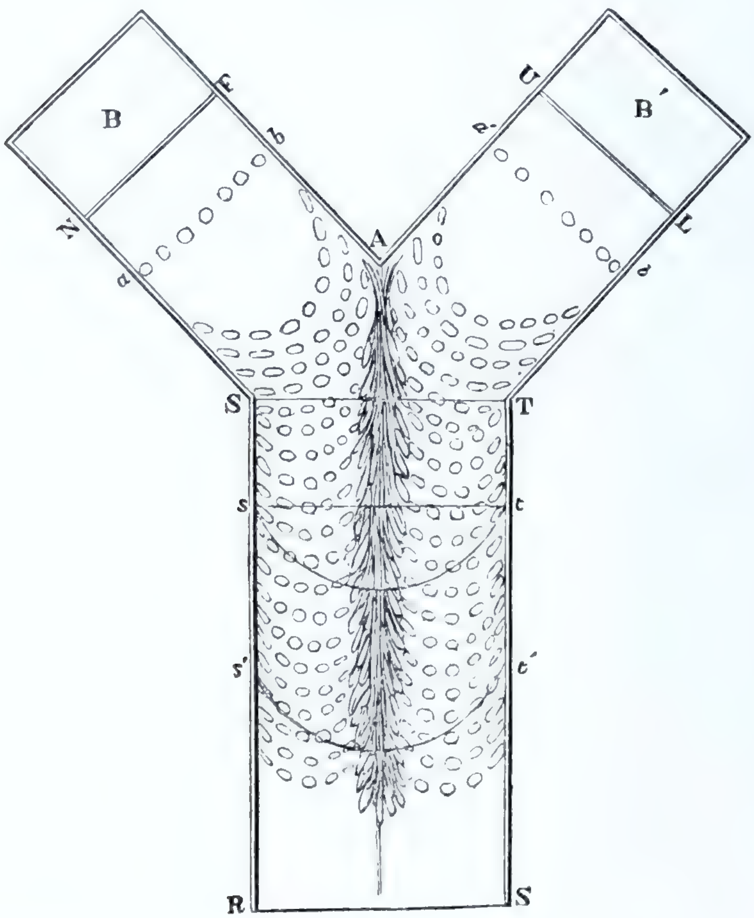
[1] Travels, p. 352.

known in this country through his important memoirs on the Mechanical Theory of Heat:—"I must now," writes M. Clausius, "describe to you another singular coincidence. I had read your paper upon the cleavage of rocks . . . . . and it occurred to me at the time that the blue veins of glaciers, which indeed I had not seen, but which had been the subject of repeated conversations between Professor Studer of Berne, Professor Escher von der Linth, and myself, might be explained in the same manner. When, therefore, I reached the Rhone glacier for the first time, I walked along it for a considerable extent, and directed my attention particularly to the structure. I repeated this on the other glaciers which I visited during my excursion. I did not indeed pursue the subject so far into detail as to be able in all cases to deduce the blue veins from the existing conditions of pressure, but the correctness of the general explanation impressed itself upon me more and more. This was particularly the case in the glacier of the Rhone, where I saw the blue bands most distinctly, and where also their position harmonized with the pressure endured by the glacier when it was forced to change the direction of its motion. You can therefore imagine how astonished I was to learn that at the same time, and on this very glacier among others, you had been making the same investigations." It ought also to be remarked, that a similar thought occurred to Mr. Sorby, from whom after his return from Switzerland one of us received a note, in which pressure was referred to as the possible cause of the veined structure of glacier ice.

A fine example of ice lamination is that produced by the mutual thrust of two confluent glaciers. The junction of the Lauter Aar and Finster Aar glaciers to form the glaciers of the Unter Aar is a case in point, and the results obtained with a model of this glacier were highly interesting. Fig. 9 is a sketch of the trough in which the experiments were made. The branch terminating at UL is meant to represent the Lauter Aar glacier; that ending at FN the Finster Aar branch. The point at A represents the "Abschwung," so often referred to in the works of M. Agassiz. B and B′ are two boxes with sluice fronts, from which the mud flows into the trough. The object was to observe the mechanical state of the mass along the line of junction of the two streams, and along their respective centres, and compare the result with the observations upon the glacier itself. The mud was first permitted to flow simultaneously from both boxes, and after it had covered the bottom of the trough to some distance below the line ST, the end of a glass tube was dipped into a fine mixture of the red oxide of iron and water, and the two arms of the glacier were

covered all over with small circles similar to those between the points *ab* and *a′b′*. The mud was then permitted to flow, and the mechanical strains exerted on it were inferred from the distortion of the small circles. The figure represents the result of the experiment. The straight rows of circles bent in the first place into curves; at the point A both streams met, and by their mutual push actually squeezed

Fig. 9.



the circles into lines. Along this central portion in the glacier itself the great medial moraine stands, and under it and beside it, as already stated, the lamination is most strikingly developed; the blue veins being parallel to the axis of the glacier, or, in other words, coinciding with the direction of the central moraine. Midway between the moraine and the sides of the glacier the structure is very imperfectly developed; and the deportment of our model, which shows that the circles here scarcely change their form, tells us that this is the result

which ought to be expected. It may be urged, that the structure is here developed, because of the sliding motion produced by the swifter flow of one of the glaciers; but some of the experiments with the model were so arranged, that both of the branch streams flowed with the same velocity; the distortions, however, were such as are shown in the figure. The case is precisely the same in nature. On reference to the map of M. Agassiz, we find a straight line set out across the Unter Aar glacier bent in three successive years into a curve; but on the central moraine, which marks the common limit of the constituent streams, we find no breach in the continuity of the curve, which must be the case if one glacier slid past the other.

§ 6. *On the "Dirt-Bands" of Glaciers*

Wherever the veined structure of a glacier is highly developed, the surface of the ice, owing to the action of the weather, is grooved in accordance with the lamination underneath. These grooves are sometimes as fine as if drawn by a pencil, and bear in many instances a striking resemblance to those produced by the passage of a rake over a gravelled surface. In the furrows of the ice the smaller particles of dirt principally rest, and the direction of the furrows, which always corresponds with that of the blue veins, is thus rendered so manifest, that a practised observer can at any moment pronounce upon the direction of the lamination from the mere inspection of the surface of a glacier. But besides these narrow grooves, larger patches of discoloration are sometimes observed, which take the form of curves sufficient in width to cover hundreds or thousands of the smaller ones. To an eye placed at a sufficient height above a glacier on which they exist, their general arrangement and direction are distinctly visible. To these Professor Forbes has given the name of "Dirt-Bands," and the discovery of them, leading as it did to his theories of glacial motion, and of the veined structure of glacial ice, is to be regarded as one of the most important of his observations.

On the evening of the 24th of July he walked up the hill of Charmoz to a height of about 1000 feet above the level of the glacier, and, favoured by the peculiar light of the hour, observed "a series of nearly hyperbolic brownish bands on the glacier, the curves pointing downwards and the two branches mingling indiscriminately with the moraines." The cause of these bands was the next point to be considered, and his examination of them satisfied him "that the particles of earth and sand and disintegrated rock, which the winds and avalanches and water-runs spread over the entire breadth of the

ice, formed a *lodgement* in those portions of the glacier where the ice was most porous, and that, consequently, the 'dirt-bands' were merely *indices of a peculiarly porous veined structure traversing the mass of the glacier in these directions.*"

Professor Forbes was afterwards led to regard these intervals as the marks of the annual growth of the glacier; he called the dirt-bands "annual rings,"[1] and calculated, from their distance apart, the yearly rate of movement. In fine, the conclusion which he deduces from the dirt-bands is, that a glacier throughout its entire length is formed of alternate segments of porous and of hard ice. The dirt which falls upon the latter is washed away, as it has no hold upon the surface; that which falls upon the former remains, because the porous mass underneath gives it a lodgement. "The cause of the dazzling whiteness of the glacier des Bossons at Chamouni is the comparative absence of these layers of granular and compact ice: the whole is nearly of uniform consistence, the particles of rock scarcely find a lodgement, and the whole is washed clean by every shower."[2] "It must be owned, however," says Professor Forbes, "that there are several difficulties which require to be removed, as to the recurrence of these porous beds." In his fifteenth letter upon glaciers, and in reference to some interesting observations of Mr. Milward's, he endeavoured to account for the difference of structure by referring it to an annual "gush" of the ice, which is produced by the difference of action in summer and winter. We are ignorant of the nature of the experiments on which this theory of the dirt-bands is founded, and would offer the following simple explanation of those which came under our own observation.

Standing at a point which commanded a view of the Rhone glacier, both above and below the cascade, we observed that the extensive ice-field above was discoloured by sand and débris, distributed without regularity. At the summit of the ice-fall the valley narrows to a gorge, and the slope downwards is for some distance precipitous. In descending, the ice is greatly shattered; in fact, the glacier is broken repeatedly at the summit of the declivity, transverse chasms being thus formed; and these, as the ice descends, are broken up into confused ridges and peaks, with intervening spaces, where the mass is ground to pieces. By this breaking up of the glacier the dirt upon its surface undergoes fresh distribution: instead of being spread uniformly over the slope, spaces are observed quite free from dirt, and

[1] "I cannot help thinking that they are the *true annual rings* of the glacier, which mark its age like those of a tree."—Appendix to Travels, p. 408.

[2] Travels, p. 406.

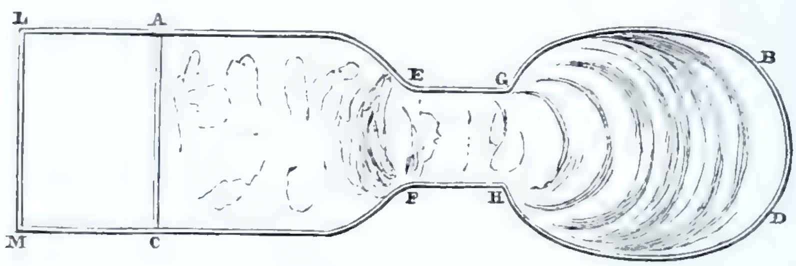
other spaces covered with it, but there is no appearance of regularity in this distribution. At some places large irregular patches appear, and at others elongated spaces covered with dirt. Towards the bottom of the cascade the aspect changes; but still, were the eye not instructed by what it sees lower down, the change would have no significance. When the ice has fairly escaped from the gorge, and has liberty to expand laterally in the valley below, the patches of dirt are squeezed by the push behind them, and drawn laterally into narrow stripes, which run across the glacier; and as the central portion moves more quickly than the sides, these strips of discoloration form curves which turn their convexity downwards, constituting, we suppose, the "Dirt-Bands" of Professor Forbes. On the Grindelwald glacier, where one of us, in his examination of the bands, was accompanied by Dr. Hooker, this change in the distribution of the dirt,—the squeezing, lateral drawing act, and bending of the dirt patches below the bottom of the ice-fall, was especially striking.

Such then appears to be the explanation of the dirt-bands, in the cases where we have had an opportunity of observing them. We have not seen those described by Professor Forbes, but the conditions under which he has observed them appear to be similar. An illustration of the explanation just given is furnished by the dirt-bands observed below the "cascade" of the Talèfre. The character of this ice-fall may be inferred from the following words of Professor Forbes, and from the map which accompanies his 'Travels.' "The structure," he says, "assumed by the ice of the Talèfre is extirpated wholly by its precipitous descent to the level of the Glacier de Léchand, where it reappears, or rather is reconstructed out of the broken fragments according to a wholly different scheme." One of the results of this "scheme" would, it is presumed, be a redistribution of the dirt, and the formation of bands in the manner described. Those who consult the map will, however, see dirt-bands marked on the Glacier du Géant, also, while no cascade is sketched upon it; but at page 167 of the 'Travels,' Professor Forbes, in referring to this glacier, says, "I am not able to state the exact number of dirt-bands between *the foot of the ice cascade* opposite La Noire and the corner of Trelaporte." Here we are not only informed of the existence of a cascade, but are left to infer that the dirt-bands begin to form at its base, as in the Glacier du Géant, and in those which have come under our own observation. The clean Glacier des Bossons, also, which was referred to by Professor Forbes, in one of his earliest letters, as affording no lodgement to the dirt, possesses its cascade (page 181), and here also we find (page 182) "that the peculiar phenomena of '*dirt-bands*' on a

great scale are not wanting, although from the dazzling whiteness of the ice they may be very easily overlooked." We make these remarks with due reserve, not having yet seen the glaciers referred to.

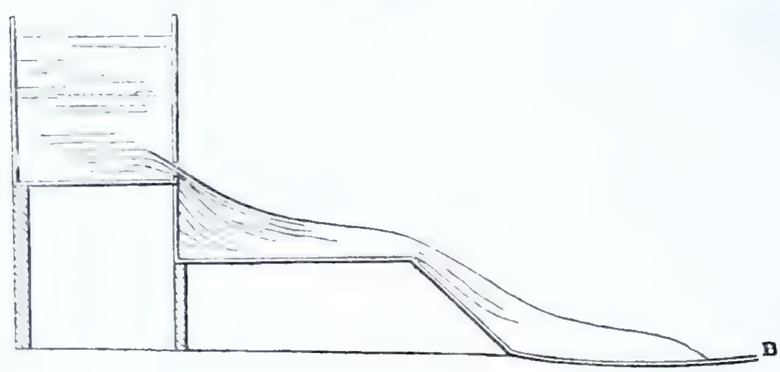
The explanation just given has been brought to the test of experiment. ABCD, fig. 10, is a wooden trough intended roughly to represent the glacier of the Rhone, the space ACEF being meant for

Fig. 10.



the upper basin. Between EF and GH the trough narrows and represents the precipitous gorge down which the ice tumbles, while the wide space below represents the comparatively level valley below the fall, which is filled with the ice, and constitutes the portion of the glacier seen by travellers descending from the Grimsel or the Furka pass. ACLM is a box with a sluice front, which can be raised so that the fine mud within the box shall flow regularly into the trough, as in the cases already described. The disposition of the trough will be manifest from the section, fig. 11. While the mud was in slow motion

Fig. 11.



downwards, a quantity of dark-coloured sand was sifted over the space, ACEF, so as to represent the débris irregularly scattered over the corresponding surface of the glacier; during the passage of the mud over the brow at EF, and down the subsequent slope, it was

hacked irregularly, so as to represent the dislocation of the ice in the glacier. Along the slope this hacking produced an irregular and confused distribution of the sand ; but lower down, the patches of dirt and the clean spaces between them gradually assumed grace and symmetry ; they were squeezed together longitudinally and drawn out laterally, bending with the convexity downwards in consequence of the speedier flow of the central portions, until finally a system of bands was established which appeared to be an exact miniature of those exhibited by the glacier. On fig. 10 is a sketch of the bands observed upon the surface of the mud, which however falls short of the beauty and symmetry of the original. These experiments have been varied in many ways, with the same general result.

In conclusion, we would remark, that our joint observations upon the glaciers of Switzerland extended over a period of a few days only. Guided by the experience of our predecessors, much was seen even in this brief period ; but many points of interest first suggested themselves during the subsequent experimental investigation. While, therefore, expressing our trust that the substance of the foregoing memoir will be found in accordance with future observation, we would also express our belief in the necessity of such observation. Indeed the very introduction of the principle of regelation, without which it may be doubted whether the existence of a glacier would be at all possible, opens, in itself, a new field of investigation. This and other questions, introduced in the foregoing pages, must however be discussed with strict reference to the phenomena as Nature presents them. Much might be said even now upon these subjects, but the known liability of the human mind to error when speculation is substituted for observation, renders it safer to wait for more exact knowledge than to hazard opinions which an imperfect acquaintance with the facts must necessarily render to some extent uncertain.

ROYAL INSTITUTION, *January* 1857.

II

ON THE AGAMIC REPRODUCTION AND MORPHOLOGY OF *APHIS*

Transactions of the Linnean Society, vol. xxii., 1858, *pp.* 193–220, 221–236.
(*Read November 5th*, 1857.)

PART I

§ 1. *Preliminary Remarks*

"J'AI souvent pensé qu'on pourrait, dans l'histoire des sciences, désigner les époques par les principales découvertes. Par exemple, 1665 seroit *l'époque de la Gravitation;* 1789, *l'époque de la méthode naturelle en Botanique;* et, *si parva licet componere magnis*, les années 1740 à 1750 seroient *l'époque des Pucerons.*"[1]

Without, perhaps, being disposed to go so far as the enthusiastic French investigator of Plant-lice, no physiologist will deny that the experiments conceived and attempted by Réaumur, but first successfully carried out by Bonnet, established facts of the highest importance, and raised questions which still disturb the very foundation of his science.

But what were these great facts, established by Bonnet and his successors or contemporaries, Trembley, Lyonet, Degeer, Kyber, and others?

If the moderns paid due attention to the labours of their predecessors, an accurate answer to this question should be found in

[1] Duvau, Mém. du Muséum, xiii. 1825.

every accredited text-book on zoology. But it will be found, on the contrary, that important errors have crept into the current conceptions respecting the reproductive processes and mode of life of the *Aphides*, and that at the present day the state of general information as to the natural history of these singular creatures is in many respects rather behind, than in advance of, that of the past generation.

Bonnet's wonderfully patient and laborious researches[1] proved, beyond all doubt, 1st, that the viviparous *Aphis* may propagate without sexual influence; 2ndly, that the brood thus produced may give rise to young in the same way; that these may repeat this asexual prolification; and so on, for as many as ten broods; 3rdly, that the viviparous *Aphides* and their brood may be either winged or apterous; 4thly, that, under certain conditions, winged or wingless males appear and copulate with oviparous females, which, in the instances observed by Bonnet, were wingless.

These are the statements put forth by Bonnet on the evidence of direct observation and experiment, and they have been confirmed by every subsequent original observer whose works I have perused. Besides these matters of fact, Bonnet states, as his strong opinion, that there is no fixed limit to the process of agamic, viviparous reproduction, and that, under favourable conditions of warmth and nourishment, it might be continued for "thirty generations" (*l. c.* p. 102), or, in other words, indefinitely.

The accurate and painstaking Degeer, who gives an elaborate account of some seventeen species of *Aphis*, affirms, as the result of his researches, "that the winged *Aphides* are never oviparous."[2] He describes at length the apterous males of certain species (P. lisse du Pin, P. du Pommier, P. du Genévrier), and shows that apterous, oviparous, and winged viviparous broods may coexist, as in *Aphis Rosæ*.

Degeer considers that, as a general rule, the oviparous females and the males are produced by alate viviparous females.

The next important original memoir on the *Aphides* is that published in Germar's 'Magazin der Entomologie' for 1815, by Kyber,[3] evidently a most careful observer, but somewhat wanting in method and clearness as a writer. Kyber is in perfect accordance with Bonnet and Degeer; and, more than this, he experimentally proved the justice of Bonnet's supposition, that the duration of the agamic

[1] Traité d'Insectologie, 1745.

[2] Degeer, Mém. sur les Insectes, 1774, vol. iii. p. 74.

[3] Einige Erfahrungen und Bermerkungen über Blattläuse von J. F. Kyber, Diacon. in Eisenberg.

reproductive power is practically indefinite, and is chiefly, if not wholly, dependent on conditions of temperature and nutrition. He says (p. 34):—

"I never saw a male in copulation with a winged female in any species. It was always the apterous females which were attacked by the males; for in many species apterous females remain among the families. Neither have I ever seen winged females lay eggs. This has, indeed, been already remarked by Degeer."

In a note Kyber adds the caution, that he has not observed more than twenty species in copulation, and does not wish to extend his conclusions beyond these.

The fourth note to this important paper contains the following remarkable observation:— . . . "The winged females especially, in which, even after frost has set in, fully-formed young may always be found, when the apterous females of the same family have long been laying eggs. On the 21st November, 1812, I still had winged *Aphides* (Haberblattläuse) in my possession, although the apterous ones had copulated and laid their eggs in September—a remarkable circumstance, without doubt, and one whence important conclusions with regard to the mode of propagation of the *Aphides* are likely to flow. Possibly many winged females survive the winter, together with their young" (p. 10).

In other parts of his memoir (p. 2 *et seq.*), Kyber adduces strong evidence in favour of the hybernation of the viviparous forms of some species, which Degeer had already proved to be the case with respect to the remarkable "Puceron des Galles du Sapin."

In the *Aphis Dianthi*, Kyber was never able to observe either copulation or oviposition; and so far from there being any natural term to the number of asexual broods which succeed one another, he states that he raised viviparous broods of both this species and *A. Rosæ* for four consecutive years, without any intervention of males or oviparous females, and that the energy of the power of agamic reproduction was at the end of that period undiminished. The rapidity of the agamic prolification throughout the whole period was directly proportional to the amount of warmth and food supplied.

Duvau, in his already cited "Nouvelles Recherches sur l'histoire naturelle des Pucerons," read before the French Academy of Sciences in 1825, states that he had carried the series of successive agamic generations in the *Aphis* of the Bean (fève) to *eleven*, which was one more than Bonnet had obtained. The process lasted seven months, and the last young was born on the 27th December, but died on the 29th. Duvau, however, kept some alive until January, and naturally

asks whether it is not probable that, under favourable circumstances, the agamic process may be continued throughout the winter. The average length of life of his *Aphides* was thirty days, or a little more; but the representative of the ninth generation lived from September 29th to December 19th, or eighty-one days. Like those of preceding observers, Duvau's researches clearly show the influence of temperature on the fecundity of the viviparous *Aphis*.

It is in Morren's in many respects valuable paper on the *Aphis Persicæ*, published in the 'Annales des Sciences Naturelles' for 1836, that the germs of the two most notable errors which have crept into the natural history of the *Aphides* may be found. At p. 76 the following passage occurs[1]:—

"The influence of temperature on these animals is obvious; in other *Aphides*, and under ordinary circumstances, the female lays her eggs when she has wings and after copulation with the male, who is winged at the same epoch. Oviposition takes place in this manner at the seventh generation for some—at the ninth, or even at the eleventh, for others; before it, female larvæ alone are produced."

Morren here supposes himself to be simply repeating what he has read. But so far as I am acquainted with the older literature of the *Aphides*, he is entirely mistaken. I can nowhere discover that either Réaumur, Bonnet, Degeer,[2] Kyber, or Duvau have observed winged oviparous females in any species; nor do the statements of any of these observers justify the belief that the sexual forms always appear after a certain number of generations. All that Bonnet affirms is, that his particular experiments came to an end accidentally after the production of a certain number of agamic generations, which is, of course, quite another matter.

When Morren details his own observations, his results are in exact accordance with those of the older observers. "In the *Aphis Persicæ*," says he, "I have very frequently seen (and I have shown the phenomenon to my colleague, M. Burgraeve) that the winged and fertilizable female never contained ova and never laid any, but that she contained little living *Aphides*, which are born fully developed, and

[1] "L'influence de la température sur ces animaux est manifeste; chez les autres pucerons, et dans les circonstances ordinaires, la femelle pond des œufs lorsqu'elle est ailée, et après un accouplement avec le mâle ailé à la même époque. Cette ponte se fait ainsi à la septième génération pour les uns, à la neuvième ou même à la onzième pour les autres; avant elle, il y a seulement naissance de femelles naissant à l' état de larves."—Morren, *l. c.*

[2] Degeer's account of the gall-forming Puceron du Pin is an apparent exception to this statement, but I believe only an apparent one. Degeer expressly states that he never saw the winged form of this species in copulation; and, besides, it is not a true *Aphis* at all.

provided with legs, proboscis, and antennæ. It was only in November that the apterous females presented eggs in their ovaries and oviducts, and, for that effect, a considerable degree of cold was necessary."[1]

Morren describes the male, female, and agamic organs of reproduction, but less completely than Von Siebold, who, in 1839,[2] carefully investigated the *Aphis Loniceræ*, and first demonstrated the existence of the spermatheca and colleterial glands in the oviparous females. Von Siebold distinguishes three forms of this species—two winged and one apterous. The large winged *Aphides* were all viviparous; the smaller, males. The apterous forms were oviparous, and the progeny of the alate females.

Steenstrup says of the *Aphides* ('Alternation of Generations,' p. 108), "The propagation of these creatures through a series of generations has been already long known. In the spring, for instance, a generation is produced from the ova, which grows and is metamorphosed, and without previous fertilization gives birth to a new generation, and this again to a third, and so on, for ten or twelve weeks; so that in certain species even as many as nine such preliminary generations will have been observed; but at last there always occurs a generation consisting of males and females, *the former of which*, after their metamorphosis, are usually winged; fertilization and the depositing of eggs take place, and the long series of generations recommences in the next year and in the same order."

In the first edition of Professor Owen's 'Lectures on the Invertebrata,' published in 1843, however, Morren's errors are adopted, extended, and enunciated as the law of propagation of the *Aphides*, in the following terms:—

"In the last generation, which is the seventh, the ninth, or the eleventh, according to the species of *Aphis*, the fertilizing influence would seem to have expired,[3] and developmental force exhausts itself in more frequent and numerous moultings, in the formation of wings, and in the modification of the female organs already described,

[1] "Or chez le puceron du pêcher j'ai vu un grand nombre de fois, et j'ai montré le phénomène à mon collègue, M. Burgraeve, que la femelle ailée et propre à la fécondation ne renfermait point des œufs et n'en pondait point, mais qu'elle renfermait des petits pucerons vivants qui naissant tout développés avec leurs pattes, leur trompe, et leurs antennes. Ce ne fut qu'en Novembre que les femelles sans ailes présentaient des œufs dans les ovaries et les oviductes, et pour cela il fallait un froid déjà assez vif."—Morren, *l. c.* p. 76.

[2] Ueber die inneren Geschlechtswerkzeuge der viviparen und oviparen Blattläuse. Froriep's Neue Notizen, 1839.

[3] This phrase is little more than a translation of a passage in Morren which will be given below.

Many males, which, like the females, acquire wings, form part of the produce of the last brood, which takes place in autumn. They rise in the air, frequently migrate in incalculable numbers, unite, and the females then produce eggs, which are glued to twigs and leaf-stalks, retain their vitality throughout the winter, are hatched in the spring, and give birth to the apterous and larviparous females, which continue to produce successive generations of similar females until the close of summer" (p. 235).

It has not been my good fortune to discover, either in Professor Owen's writings or those of his predecessors, any evidence in support of the singular statement contained in the last paragraph of this citation, which is incorrect in all important respects, and has, indeed, been omitted in the second edition of the 'Lectures.'

Mr. Walker, in the first of his long and valuable series of papers on the *Aphides* (Annals, vol. i. 1848, p. 259), writes thus :—

"I am indebted to my friend Mr. Haliday for the following translation of an extract from Erichson's Bericht, &c., 1844, Ent. Zeitung, pp. 9, 81, 133, 410. Ratzeburg observed a species of *Aphis* on the Birch, which continued to produce a living progeny from August into winter without either male or female appearing. Bouché and Kaltenbach, in explanation, remark that the males in this family are not always winged. However, in the May following, Ratzeburg, continuing his observations, found the winged females, and afterwards (in October) winged males also, which paired with them. The species was then identified as *A. oblonga*, Von Heyden. For the male to pair with a winged female (continues Mr. Walker) is a very unusual case among *Aphides*."[1] In fact, I have hitherto found, in Mr. Walker's long list of 101 species, no case of an oviparous winged

[1] On turning to Ratzeburg's notice in the 'Entomologische Zeitung,' 1844, p. 410 (Fortgesetzte Beobachtungen über die Copula der Blattläuse), which is the last word of the correspondence between Kaltenbach, Bouché and himself on this subject, I find his precise words to be these :—"Wie gross war daher mein Erstaunen, als ich bei meiner ersten, nach der Rückkehr angestellten Excursion, am 22 October gleich auf den ersten Blick unter der Menge von *ungeflügelten Individuen*, welche die des vorigen Jahres bei weitem übertraf, auch *geflügelte Puppen* und *geflügelte Männchen* bemerkte, und wie gross war meine Freude, auch gleich darauf mehrere der letztern in der Begattung zu finden, also in einem Acte, den ich bei Blattläusen selbst noch nicht hätte beobachten können." Subsequently, Ratzeburg states that he was able to observe the copulatory process early and late, at any time between the 22nd October and the 16th November.

It will be observed that there is not a word here about such winged females as Ratzeburg, in a preceding passage, states he saw in May of the same year. The winged pupæ are apparently, from the context, the pupæ of the males, and the forms with which the winged males copulated were the wingless females. So that here, as in all other supposed cases of winged, oviparous true Aphides I have looked into, the evidence, when closely examined, breaks down.

female observed by himself. Mr. Walker states as a known fact, that *Aphis Rosæ* habitually lives through our mild winters.

In his work on 'Parthenogenesis' (1849), Professor Owen modifies his previous statement so far as to say, in a note (p. 59), that the perfecting of the female generative organs in *Aphis* "is not attended by the acquisition of wings; or if they be developed in the oviparous female, they soon fall. I have, however, retained them in the diagram for a better illustration of the analogy. Many of the virgin viviparous *Aphides* acquire wings, but never perfect the generative organs."

The diagram referred to exhibits two figures, (*h*) and (*i*), which, for anything that appears in the text, might be taken to be the author's representation of male and female *Aphides*. On comparing them with the illustrations of Morren's memoir, however, it is at once obvious that they are copies of his figures 1 and 2, of which fig. 2 does really represent a male; while fig. 1, on the other hand, is not an oviparous, but a viviparous female. In the explanation of his figures, Morren indeed merely says of fig. 1, "Femelle vue en dessous;" but it requires no great amount of attention to his text to observe his distinct statement (already quoted), that the winged female is viviparous, and not oviparous. I am obliged to be thus particular in explaining these unusual circumstances, as otherwise the existence of a typical figure of a winged oviparous female *Aphis*, in the work of an accredited author, might be brought forward as conclusive evidence of the ordinary occurrence of such females.[1]

When the natural history of the *Aphides* is freed from the mythical additions which have accumulated around, and obscured it, I believe

[1] Professor Owen, in the last edition of his 'Lectures on the Invertebrata,' p. 410, quotes Léon Dufour as having witnessed the coitus of the male Aphis "with the winged female." The reference is to "Dufour, Léon, in Annales des Sciences Naturelles, vol. i. 1844." I have carefully, and more than once, scrutinized this volume of the 'Annales,' without having been able to discover the passage referred to. Léon Dufour has, in fact, two memoirs in the first volume of the 'Annales' for 1844. The first is on the "Anatomie générale des Diptères;" the second, "Histoire des Métamorphoses et de l'Anatomie du *Piophila Petasionis*." As might be expected, there is no reference to the *Aphides* in either of these papers.

Finally, the authors of the article "Hémiptères" in the 'Suites à Buffon' (1843), p. 600, quote De la Hire as their authority for saying that the oviparous female *Aphis* is winged. I have examined the passage cited (Histoire de l'Acad. Royale des Sciences, 1703), however, and I find only this :—

"M. de la Hire *croit* que les pucerons vivent une année entière, et que pendant l'hiver ils se retirent dans des trous, d'où ils sortent au printems pour pondre leurs œufs, comme le font les mouches ordinaires."

the following propositions may be said to be established on good evidence:—

1. Ova deposited by impregnated female *Aphides* in autumn are hatched in the spring.

2. From these ova, viviparous, and in the great majority of cases apterous, forms proceed.

3. The broods to which these give rise are either winged or apterous, or both.

4. The number of successive broods has no certain limit, but is, so far as we know at present, controlled only by temperature and the supply of food.

5. On the setting in of cold weather, or in some cases on the failure of nourishment,[1] the weather being still warm, males and oviparous females are produced.

6. The males may be either winged or apterous.

7. So far as I am aware, there is no proof of the existence of any exception to the law that the oviparous female is apterous.

8. Viviparous *Aphides* may hybernate, and may co-exist with oviparous females of the same species.

So much by way of clearing the ground. I now proceed to the particular subject of this paper, which is, primarily, to describe the nature of the process by which the agamic young arises within the body of its viviparous parent. But very few investigators have applied themselves to this question, and those who have are unfortunately in diametrical contradiction to one another as to the most important points.

Professor Leydig published a notice on this subject in the 'Isis' for 1848, which I have not seen; but subsequently his views, fully stated and accompanied by figures, were promulgated in Siebold and Kölliker's Zeitschrift for 1850, vol. ii. Heft 1. He maintains "that the germ of the (viviparous) Aphis is developed out of cells, and its embryo is as much composed of cells as one which has proceeded from a fecundated ovum" (*l. c.* p. 65). And he particularly details the manner in which one of the large cells contained in the terminal chamber of the proliferous organ of the viviparous *Aphis* becomes detached, enlarges, and is converted into the embryo. Although Leydig does not absolutely say as much, his observations lead to the conclusion that there is no histological difference between the agamic germ in its youngest state and a true ovum at a corresponding period.

Von Siebold implies, and Professor Owen, Victor Carus, and the

[1] See Hausmann's "Beiträge" in Illiger's Magazin, Bd. 2.

late Dr. Waldo Burnett assert, with different degrees of distinctness, on the contrary, that there is a clear histological difference between the primary germs of the viviparous *Aphis* and true ova,—Carus and Burnett reiterating their opinions even since the publication of Leydig's views. Finally, Mr. Lubbock, in his late valuable memoir on *Daphnia* (Phil. Trans. 1857) has expressed his inability to find any germinal vesicle in the germs of the viviparous *Aphis*, and, so far, may be ranked among Leydig's opponents.

I have recently resumed some investigations commenced two or three years ago on this interesting subject. My object was originally purely morphological,—the *Aphis* suggesting itself as a very convenient subject for working out the general development of *Insecta*; but I have found myself unable to refrain from wandering out of my direct course, and attempting to further the solution of the great problem of Agamogenesis, or asexual reproduction.

My observations are in the main in accordance with those of Leydig. On many minor points, however, we are at variance; and besides this, there are matters of great interest, upon which Leydig does not touch, but on which I hope to be able to throw some light. For, besides yielding an answer to the question as to the existence or absence of any histological distinction between a bud and an ovum, the investigation of the viviparous and oviparous *Aphides* affords decisive evidence as to the soundness of certain explanations of the phenomena of Agamogenesis in general; and finally, the study of the general development of *Aphis* furnishes data of great importance in Articulate Morphology.

I propose in the present memoir to follow out these lines of inquiry. I will, in the first place, describe the minute structure of the essential reproductive organs or "Pseudovaria" of the viviparous or agamic female; and the development of its germs or pseudova (as I propose to term them) will be considered. Secondly, the reproductive organs of the oviparous female and the development of the ova will be described. Next, I shall speak of the manner in which the proliferous apparatus or pseudovarium of the viviparous female is developed within the germ; and I shall compare together the agamic and sexual reproductive processes. I shall then endeavour by means of these facts to refute a hypothesis which has been offered in explanation of Agamogenesis; and, finally, I propose to consider the Morphology of the *Articulata* so far as it is elucidated by Development.

The species of *Aphis*, the reproductive organs of whose viviparous form I am about to describe, appeared this autumn upon a plant of

the Ivy-leafed Geranium which hangs in my study, and for the last two months has been regularly giving rise to broods, sometimes winged and sometimes apterous, without any appearance of males or females. With respect to the external characters of the reproductive organs, I have nothing of importance to add to Siebold's or Morren's description.

§ 2. *The Development of the Pseudovum*

The terminal chamber of any of the cæca of the pseudovarium is a rounded or oval body (Pl. XXXVI. [Plate 1] fig. 1, A), united by a delicate ligament (*a*), proceeding from its free end, with the ligaments which pass from the other cæca of the same side, to form the common pseudovarian ligament. The wall of the chamber is a delicate transparent membrane (*b*), in which, here and there, rounded endoplasts (or nuclei) are imbedded; while others lie on its inner side, constituting a sort of epithelial layer (*c*) continuous with the contents of the chamber. These, when perfectly unaltered, are constituted by a homogeneous pale periplastic substance (*d*), containing about a dozen clear spheroidal cavities (*e*) whose walls are a little denser than the rest of the periplast. The cavities have on an average a diameter of $\frac{1}{3000}$th of an inch. In the centre of each is a rounded opaque body (*f*) like one of the endoplasts of the wall of the dilatation, and, indeed, obviously of the same nature.

In whatever fluid I have examined this tissue, it began after a time to alter. In the very weak syrup which I ordinarily employed, the change consisted partly in the slightly increased definition of the walls of the clear cavity, but more particularly in the breaking up of the periplast into spheroidal masses, each of which contained a single vesicle and its endoplast.[1] The resemblance of such a body to an ovum with its germinal vesicle and spot is complete; nor would it be possible for any one ignorant of the origin of the body to say that it was other than an ovum. Water instantly alters the appearance of the tissue, completely destroying its distinctive character. Dilute glycerine shrivels up the vesicles and alters the appearance of their central endoplast, probably by endosmose. Acetic acid renders the periplast dark, and gives an exceedingly marked definition to the parietes of the vesicle. To see the appearances I have described as normal, the part must be examined perfectly fresh, and in a solution of sugar neither too dilute nor too concentrated.

In certain specimens the contents of the lower part of the terminal

[1] Leydig (*l. c.* p. 63) appears to regard this as the first state of the ovigerms, and he has overlooked the epithelium.

chamber are different from those of the upper. As much as a third of the whole chamber may be occupied by a mass of periplast containing only a single clear vesicle. Such a condition is figured in fig. 1, Pl. XXXVI. [Plate 1] fig. 2 exhibits a further advance in the same direction; the mass which, from its close resemblance to a true ovum, I have called a pseudovum, having enlarged so much as nearly to equal the contents of the terminal chamber, from which it is distinguished by a slight constriction. In figs. 3 and 4, the constriction has become more marked, until at length a penultimate chamber is formed, connected only by a narrow neck with the terminal one, fig. 4. It is on an average about $\frac{1}{500}$th of an inch in diameter. The epithelial layer *(c)* of its wall is ordinarily well developed, and, when water is added, swells up, so as to separate the periplastic substance of the pseudovum from the wall. The periplast itself exhibited no structure, and appeared unchanged, except in size. The clear vesicle was sometimes unchanged, sometimes enlarged, but otherwise unaltered. Of its endoplast I was sometimes unable to discover any trace; on other occasions I found a few granules in its place (fig. 3); and, once, two particles, each rather more than half its diameter, appeared to lie side by side in the interior of the vesicle.

The marked contrast between the perfect distinctness of the endoplast in the vesicles contained in the ultimate pseudovarian chamber, and its apparent absence in the very similar vesicle of the mass contained in the penultimate chamber, or in the lower part of the last one, was the more striking, as the two could be readily compared under the same circumstances and in the same field of view.

Finally, the vesicle itself ceases to be visible (fig. 4), and the penultimate chamber contains only its epithelium and a mass of apparently structureless substance;—I say apparently structureless, because the addition of water made the mass more clear, and at the same time rendered an irregular areolation and scattered granules visible in its substance. Whether the areolæ are the outlines of delicate vesicles, and the granules their endoplasts, or not, are points which I could not satisfactorily determine; at any rate, I could never observe anything like the regular structure observable in the contents of this chamber when a little larger.

Fig. 5 represents such a chamber, $\frac{1}{417}$th of an inch in length. The endoplasts of the wall are seen lying in or upon it, and occupying its interior is a distinct oval mass of substance agreeing in appearance with the periplast of the pseudovum, but distinguished from it by containing a great number of clear spheroidal cavities not more than $\frac{1}{3200}$th of an inch in diameter, each of which contains a central

endoplast of not more than $\frac{1}{10000}$th of an inch. These cavities are closely packed, but not flattened against one another. The walls of the cavities react differently on the addition of acetic acid to the rest of the periplast, becoming darker and more sharply defined. In fact, each cavity is what is commonly termed a nucleated cell, while the intervening periplast is the so-called intercellular substance.

I have here stated merely the histological facts which may be observed by any one who will take the trouble to examine with sufficient care the ultimate and penultimate pseudovarial chambers of a few viviparous *Aphides*. Of the existence of these states, and that the order in which I have detailed them fairly represents the order in which they succeed one another in nature, I have no doubt; and I therefore look upon it as an established fact, that the primary steps in the agamic development of *Aphis* are, first, the enlargement of the periplast around one of the pseudovarian vesicles, and its detachment as a separate body, which, from its resemblance to an ovum, I will call a "pseudovum;" secondly, the contemporaneous formation of a distinct chamber—the penultimate chamber of the pseudovarium; thirdly, the disappearance of the vesicle of the pseudovum, and the conversion of the latter into a germ-mass composed of cells imbedded in intercellular substance and containing minute endoplasts.

I should be sorry, however, to express an opinion as to the exact nature of the process by which these changes are effected, with anything like the same degree of confidence. Three hypotheses present themselves:—

1st. The pseudoval endoplast divides and subdivides, so as to give rise to the endoplasts of the germ; or—

2nd. The pseudoval endoplast is resolved, and the endoplasts of the germ are developed autogenously in its periplast; or—

3rd. The pseudoval endoplast disappears, and the endoplasts of the germ are supplied from the epithelium of the walls of the pseudovarial chamber.

Of these three hypotheses, I strongly incline towards the first, as most in accordance with what we know of histological development in general. The whole progress of modern research, in fact, goes to show that cells and endoplasts hardly, if ever, arise autogenously, but are the result of the subdivision of pre-existing cells and endoplasts. If this be the case, however, the second hypothesis is excluded, and the third is improbable in itself, and is supported by no evidence. In the absence of such evidence, the marked contrast in size and appearance between the epithelial endoplasts of the penultimate

chamber and those of the germ tends to show that the two have no direct relation to one another.

Those who have followed the details of the development of the pseudovum and its resulting germ, given above, will not fail to admire the clear insight of Morren, when he affirmed that the agamic offspring of *Aphis* was developed by "the individualization of a previously organized tissue." A more neat and expressive definition of the process could not be given: and as Morren nowhere entertains the absurd doctrine that an organized tissue must be as complex as "mucous membrane" or "muscular fibre," which has been attributed to him, the criticisms to which his views have been subjected on this ground are sufficiently baseless. No one will pretend to deny that the pseudovarium is "organized," nor that the pseudovum is a portion of it which has become "individualized." But I subjoin Morren's words, that the reader may form his own judgment as to his merits:—

"À dire vrai, je me refuse à émettre une opinion au milieu d'un tel dédale, et je tiens pour plus philosophique d'avouer son ignorance dans un phénomène où la nature nous refuse même l'apparence d'une explication. S'il fallait une explication à toute force, j'admettrais que la génération se fait ici comme chez quelques entozoaires, *par individualisation d'un tissu précédemment organisé.* La génération n'est pas pour cela spontanée: une *génération spontanée* doit être la production d'un être organisé de toutes pièces, lorsque les élémens inorganiques se réuniront pour produire un animal, une plante. Cette génération est impossible et n'a jamais lieu. Une *génération équivoque* est celle où des tissus organisés préalablement par un être déjà pourvu de vie, s'individualisent, c'est à dire, séparent de la masse commune et participent encore, après cette séparation de l'état dynamique de la masse, c'est à dire, de sa vie, mais à son propre profit. C'est ainsi qu'un tissu produit un entozoaire.[1] C'est de la vie continuée. Mais supposez que la vie ait assez d'énergie pour imprimer au tissu que s'individualise la forme de l'espèce productrice, et vous avez la génération des pucerons. Cette énergie se perd au bout de quelques générations, et une nouvelle impulsion devient nécessaire, c'est celle du mâle.

"Voilà à tout hasard, une hypothèse que dans ma jeunesse j'aurais embrassée avec plaisir; mais aujourd'hui je préfère douter: les faits que j'ai exposés plus haut valent mieux qu'une théorie."—Morren, sur le Puceron du Pêcher, Annales des Sc. Nat. série 2. vi. 1836, p. 90.

[1] I need hardly remark, that no evidence of the development of *Entozoa*, in the way supposed by Morren, is in existence.

§ 3. *Description of the Oviparous Female Aphis and of the Development of the Ovum*

Throughout the two months during which the Ivy-leafed Geranium, on which my viviparous *Aphides* are living, has been in my possession, neither males nor females have made their appearance. Therefore, being extremely desirous to compare the process of the development of the germ with that of the ovum, before completing this paper, I began in the last days of October to seek for oviparous females of some other species.

An Oak-teee in the Zoological Gardens at length supplied me with that which I sought. The small twigs and leaves afforded habitation to a number of minute wingless *Aphides*, all so nearly equal in size that I did not doubt their non-viviparous, and hence in all probability their oviparous character.

Microscopic examination fully confirmed my suspicions; for not only were the *Aphides* full of ova, but I found multitudes of similar ova adhering to the plant in the axils of the leaves, and more particularly between the outer bracts of the buds.[1]

These *Aphides* were very different from my viviparous species. They were about $\frac{1}{12}$th of an inch in length. The general hue of the body was pale green; but it was diversified in the dorsal region by four longitudinal rows of blackish rounded spots, one spot in each row being seated on the tergum of most of the somites, from the prothorax backwards. Hence there were nearly as many transverse rows of four spots each, as segments of the body. The two median spots in each row were larger, and situated close to the middle line. The external spots were more upon the sides of the body. The spots upon the mesothorax, and thence to the sixth abdominal somite inclusive, were the largest and most conspicuous. Each spot was constituted by a dark elevation of the integument, which supported a tuft of long setæ, knobbed at their extremities like the glandular hairs of certain plants. The hairs were not confined to these localities, however, but were scattered over the head and other parts of the body. The eyes were red, and produced into a small tubercle on their posterior margins. The distal portions of the antennæ, and the

[1] I do not think that my *Aphis* of the Oak is identical either with that described by Réaumur, or that described by Bonnet. None of my specimens attained the size of theirs, nor do either of those writers mention the peculiar dorsal markings of my species: furthermore, the proboscis in both Réaumur's and Bonnet's was long; it mine it is very short. The proper specific names of both the *Aphides* alluded to in this memoir will be discussed in a final note.

tarsi, were blackish. The antennæ were not more than equal to half the body in length; they were seven-jointed, the penultimate joint being somewhat swollen at its extremity. Both this and the preceding and following joints were so sculptured as to appear, at first, minutely annulated. The basal joint was the thickest of all; the second less thick, but stronger than the others. The proximal half of the antennæ was sparsely setose. The promuscis was short, extending, when deflexed, no further than the posterior edge of the prothoracic sternum. The abdomen tapered into a cone beyond its sixth somite, on whose dorso-lateral region the very short trumpet-mouthed siphons were situated. The abdomen was terminated by two subcylindrical rounded setose tubercles, of which the lower was the larger. They had the anus between them, and acted as anal valves. The posterior limbs, when fully extended, hardly reached beyond the end of the abdomen.

The eggs when first laid are of a dark green hue and very soft; afterwards they appear to become black.

The vulva of the oviparous *Aphis* (B) opens between the eighth and ninth abdominal sterna, the eighth (8) being a little prolonged, so as to form a sort of inferior lip to the vaginal aperture (Pl. XL. [Plate 5] fig. 1). The vagina (C) is a thick-walled tube provided with a layer of external transverse, and internal longitudinal, striated muscles. After entering the sixth abdominal somite, it divides into two branches—the oviducts (DD), whose walls exhibit the same muscularity, but are less thick. Both vagina and oviducts are lined by a well-developed epithelium.

The oviducts divide into four ovarian cæca, whose delicate structureless wall is unprovided with muscles, and lined by a columnar epithelium. Each cæcum is ordinarily divided by constrictions into six chambers. Of these I found the posterior (that nearest the vulva) (E) always empty, and of nearly the same length, though of a much smaller diameter than that which precedes it, or the fifth from the apex of the ovarium. This fifth chamber (F) always contained a fully formed ovum, provided with a chorion and an opaque coarsely granular yelk.

The fourth chamber (G) is smaller than the fifth; it contains a coarsely granular vitelline mass in which no germinal vesicle can be perceived, and which ordinarily has no investing membrane.

The third chamber (H) is still smaller; and its contents are usually only slightly granular, so that the germinal vesicle and spot of the ovum in this chamber are beautifully distinct (fig. 2).

The second chamber (I) is the smallest of all; the germinal

vesicle and spot of its rudimentary ovum can be easily seen; and but very few fine granules are deposited in the substance which will eventually form the yelk.

A clear cord-like mass (*q*), commonly divided longitudinally, so as to appear double, traverses this chamber, and can be traced into the next.

The apical chamber (K) is as large as the third, but is longer transversely than longitudinally, while the reverse is the case with the third chamber. Its outer wall is formed by a continuation of the same structureless membrane as that which constitutes the rest of the cæcum. The epithelium (*p*), which is particularly thick in the upper part of the second chamber, especially at the neck or constriction between the first and second, is suddenly attenuated as it spreads on the inner face of the wall of this chamber, and becomes very thin from the flattening of its cells. From having the characters of a cylinder-, it takes those of a pavement-epithelium.

It is at first extremely difficult to understand the nature of the contents of the apical chamber. All its anterior part appears to be filled with about a dozen closely appressed bodies (*l*), which, if examined without due attention, or under a low power only, may easily be confounded with ova. Each of these bodies has a sort of wedge shape, such as would result from the compression of rounded masses in a spherical envelope which they nearly fill. Its apex is turned inwards; its base outwards. Each consists of a thick transparent outer coat closely investing a denser and well-defined membranous sac. The latter contains a clear substance, in which many irregular granules are embedded. The lines of separation between the appressed sides of these bodies are well seen, either in a sectional or a superficial view. In the latter case, they appear as polygonal meshes; in the former, as lines separating the bodies from one another, and bounding their curved bases on the side of the epithelium. On tracing the lines of separation towards the central interval between the ends of these bodies, they become lost, and a mere clear, homogeneous substance seems to occupy the whole central part of the chamber; but on carrying the eye backwards, this clear mass is seen to be continuous with the two cords which I have above described as entering the second chamber (Pl. XL. [Plate 5] fig. 3).

The histological constitution of these bodies is at once sufficient to convince the observer that they are not ova, and I regard them as glandular masses which secrete the matter of the clear cord-like bodies which descend into the second and third chamber.

The ova themselves, or rather the rudiments of the future ova,

are not always to be seen with ease; and if the epithelium of the lower part of the apical chamber has become much altered, they cannot be detected: for they are visible exclusively in this part of the chamber, of whose epithelial cells they are, as I believe, merely a modification. However this may be, germinal vesicles and spots of all sizes intermediate between that of the ovum of the second chamber and that of an ordinary epithelial cell are seen in close contact with the parietes of the chamber. I have detected as many as six in this position. When the chamber is subjected to compression they may be set free, and are then seen to be surrounded by a zone of clear substance, the rudimentary vitellus. Under similar circumstances, the "glandular bodies" may also be isolated; when they present themselves as vesicles surrounded by a clear homogeneous substance, which is frequently prolonged at their apical extremity. It is gradually dissipated, and the inner sac set free by the action of water.

I have not seen any ovarian ligament in the oviparous *Aphis*.

The structure which I have described was wholly unexpected and new to me; and I am not aware that anything similar has yet been noticed in the ovaria of Insects.[1] I am inclined to believe that the glandular bodies contribute directly to the formation of the vitellus, because I have more than once seen cases, like that figured in Pl. XL. [Plate 5] fig. 3, where the clear cord-like body appeared to pass directly into the mass of the ovum. There was always a widely open communication between the first and second, and between the second and third chamber; but the passage between the third and fourth was closed by the meeting of the epithelial lining. Does each ovum, as it is given off from the ovary, and passes backwards, carry with it a gelatinous mass, the product of one half of the glandular bodies, and only cease to be connected with these glands when it has taken the third place?

Three cæca open into the dorsal side of the lower part of the vagina; of these the anterior single one is the spermatheca; the posterior pair are the colleterial glands (Pl. XL. [Plate 5] fig. 1, *m*, *n*).

The spermatheca (*n*) is a sac with a narrow neck, dilated at its extremity, which opens considerably in advance of the colleterial glands, while its enlarged end lies between them. The duct of the

[1] Unless, as I am strongly inclined to suspect from Leydig's description, and from a hasty examination on my own part of the ovaria of *Coccus*, the corresponding chamber of that insect's remarkable ovaria presents a similar structure. (See, however, the note which concludes this paper.)

spermatheca has thick walls continuous with those of the vagina; but its dilated portion is thin, and has a yellowish colour. It contains a multitude of large filiform spermatozoa bent upon themselves, and is very tough and resisting.

The colleterial glands (*m*) are subcylindrical, but are constricted inferiorly where they open close to the vulva. They consist of a delicate structureless coat lined by a thick layer of granular substance, whose cellular composition is very indistinct in the fresh state, but becomes obvious on the addition of acetic acid.

The interior of the gland contains a clear, viscid, strongly-refracting substance, apparently separated from the epithelial lining by a membranous layer. I am in doubt, however, whether this apparent membrane be anything more than the folded and wrinkled outer layer of the viscid matter. When the *Aphis* is suddenly placed in glycerine or subjected to slight pressure, a drop of the colleterial secretion not unfrequently exudes and manifests its viscidity by leaving a long trail.

The fully-formed ovum (Pl. XL. [Plate 5] fig. 1, F) measures about $\frac{1}{70}$th of an inch in length. It is oval, rather smaller anteriorly, and of a deep green hue, in consequence of the colour of the yelk. The chorion is a tough transparent membrane, about $\frac{1}{9000}$th of an inch thick, and presents no external sculpturing or internal structure. Internal to the chorion is a delicate vitelline membrane which immediately invests the yelk. It is, however, connected with the chorion posteriorly. When the egg is heated with caustic potass, the yelk is driven away from the sides (eventually dissolving), and with it the vitelline membrane on the sides and at the anterior part of the ovum; posteriorly, however, I always found it adherent. The yelk itself is very coarsely granular; so that there would be no chance of discovering the germinal vesicle, even if it existed.

The recent observations of Leuckart and Meissner on the micropyle of the ovum in Insects naturally induced me to look for such a structure in the egg of *Aphis*.

Leuckart, in his elaborate essay, clearly shows that the micropyle may be single or multiple, and may occur at either or both poles of the egg; but unfortunately he gives us less information respecting the ova of the Homopterous *Hemiptera* than regarding those of any other great group of Insecta. *Cercopis*, in fact, is the only genus of this division in which he has observed the micropyle with certainty, and here there are two—one on each side of the anterior pole.

The anterior extremity of the chorion in *Aphis* (Pl. XL. [Plate 5] fig. 4, B.) presents a small conical papilla, in which I have been unable

to discover any aperture. Internally, however, the corresponding surface of the chorion appears as it were rough and uneven; and when caustic potass is added, it, like the rest of the inner surface of the chorion, exhibits a very curious marking, as if so many circles or more irregular figures were impressed upon it. The thickness of the papilla is about $\frac{1}{4000}$th of an inch; and in young ova a delicate filiform appendage more than once appeared to be continuous with it: this, however, was invariably absent in fully-formed ova.

At the opposite pole (fig. 4, A), the ovum presents a curious appendage, about $\frac{1}{530}$th of an inch in length. When the ovum is in its natural position within the ovary, the epithelium of the latter, which closes over it below, leaves a sort of chamber in which this appendage, ordinarily more or less closely applied against the chorion, is received.

When the ovum is extracted, the appendage appears like a rope with loosened strands, or a closely-plaited membrane, and is seen to be coated with a clear gelatinous substance, in which many minute rod-like filaments of about $\frac{1}{4000}$th of an inch in length are imbedded. Treated with caustic potass, this clear substance and its imbedded particles are dissipated, and the central cord becomes less distinct; but I have never yet seen it dissolved, and sometimes it seems altogether to resist the reagent. The rounded tubercle of the chorion to which it is attached, however, now clearly exhibits a central funnel-shaped body, continuous with the axis of the appendage, and appearing like a canal (fig. 4, C).

Is this a micropyle, and what is the nature of the appendage? I regret that I have not the leisure to pursue the inquiry far enough to answer this question satisfactorily; but I incline to think that the micropyle is really situated here.[1]

The albuminous papilla surrounding the bundle of spermatozoa in the impregnated ova of *Musca*, *Dexia*, and *Melophagus* (Leuckart, *l. c.*

[1] After describing the cup-like micropyle at the anterior pole of the ovum of the Louse, Leuckart (*l. c.*) goes on to say—"Besides this micropylar apparatus at the anterior pole, there is at the posterior pole of the ovum a structure which attracts attention. It may be described as a blunt cone, which is attached rather on one side of the centre of the posterior pole, and has acquired a peculiar striated appearance by reason of its longitudinal folds, and band-like thickenings. The interior diameter of this structure measures $\frac{1}{50}'''$; the upper is less, about $\frac{1}{85}'''$; and the length is about the same. A hollow space is contained within this body, so that it might be compared to a bell; but it seems as if from the roof, or cupola, as it might be termed, of this bell, a number of closely appressed elevations and points depended. With respect to the import of this remarkable apparatus, I will only throw out the supposition that it is an apparatus of attachment. For a long time I thought I had dis covered in it a second micropylar apparatus; but I renounced this view when I was unable to discover any aperture in it." (p. 140.)

pl. 7, figs. 1, 2, 4, 5), reminds one strongly of the envelope of the appendage in *Aphis.*

The micropyles of *Libellula*, *Dexia*, and *Musca*, again, exhibit a sort of "mouthpiece" formed by a prolongation of the chorion surrounding the micropylar aperture.

The account which I have given of the reproductive organs of the oviparous *Aphis* is in general agreement with that of other observers. Morren describes the reproductive organ of the wingless oviparous female of *A. Persicæ* thus:—

"The ovigerous cæca well deserved their name; for no fœtuses were any longer visible in them. Each was exactly composed of three chambers, of which the first or terminal was enlarged and spherical, and filled with twelve to twenty-four little well-formed ova, yellow in the centre, and white peripherally. These ova descended into the second chamber, and then elongated and enlarged; but in general they acquired their hard covering only in the third or last chamber, which in all the females was occupied by a very large ovoid greenish ovum. These ova became covered at the same time with the sebific liquid; for some were seen to be provided with a little appendage intended to fix them to the bodies in which the parent lays them. This appendage was mucous, and arose from a thickened viscous liquid." (*l. c.* p. 89.)

I recognize in Morren's "twelve to twenty-four ova" the ovarian glands which I have described. His microscope was obviously inadequate to show him the true ova; but it seems difficult to suppose that in this species there is, as he maintains, neither colleterial glands nor spermatheca. His objection to Dutrochet's statements appears to me to be well founded, for Dutrochet examined a viviparous female; but I strongly suspect that he has himself overlooked the "sebific" apparatus in the oviparous forms.

Von Siebold states that the ovarian cæca of the oviparous *Aphis Loniceræ* are divided into only two chambers:—

"In the undeveloped state the whole tube forms only a simple pyriform appendage of the oviduct; but as development proceeds, the upper globular chamber becomes by degrees separated by a constriction, and at the same time a great difference makes its appearance between the upper and the lower chambers: for the lower chamber contains a finely granular mass which gradually becomes modelled into an oval egg; the upper chamber, on the other hand, is filled with vesicular bodies, in which smaller vesicles containing a nucleus are distinguishable. If these bodies are to be regarded as germs of ova (Wollte man diese blasenförmigen Körper als Eier-

keime betrachten), we may assume that these *Aphides* were capable of bringing forth more than eight ova."

Von Siebold then goes on to describe the colleterial glands, and the spermatheca, which had not before been seen. If the ovaries of *Aphis Lonicerœ* are not constructed on a totally different plan from those of the species I have described, it is, I think, pretty clear that Von Siebold, like Morren, has mistaken the ovarian glands for the rudiments of the ova. Indeed, his phraseology indicates that he himself had no great confidence in his interpretation of the parts.

§ 4. *The Development of the Pseudovarium*

In the viviparous female, the germ increases in size, and gradually becomes separated from the terminal chamber by the successive development and separation by constriction of new pseudova. The number of chambers between the terminal one and that nearest the vagina, therefore, varies until it attains its maximum, which is necessarily regulated by the ratio between the time required for the perfection and birth of a larva and the rate at which new pseudova are detached from the pseudovarium. In the species of *Aphis* which I examined, I found ordinarily four or five such chambers. Germs between $\frac{1}{400}$th and $\frac{1}{50}$th of an inch in length presented the following characters (Pl. XXXVII. [Plate 2] fig. 1):—They exhibit a central darkish matter, surrounded by a clear cortex. The latter is composed of a single layer of a substance similar in appearance to that composing the mass of the germ above described, while the central substance is obscured by a number of minute granules which hide its internal structure. Nevertheless, I have occasionally detected what I believe to be endoplasts, scattered through its substance, as in Pl. XXXVII. [Plate 2] fig. 1, which represents a germ in this stage treated with very dilute acetic acid; and as in a more advanced condition we shall find such bodies easily recognizable, I do not doubt that the central substance has the same fundamental composition as the peripheral layer. The central mass, it will be observed, completely simulates the vitellus of an impregnated ovum; and I will therefore term it a "pseudovitellus." The peripheral clear layer is, on the other hand, in all essential respects comparable to a blastodermic vesicle; and I see no reason why it should not be called a blastoderm, since the term is not necessarily confined to the product of impregnation.

In a more advanced condition (fig. 3), the blastoderm has become thicker in all parts, so as to consist of at least two or three layers of

"cells;" but the thickening shows itself, especially upon one side of the distal end of the germ (that turned towards the vagina), where the blastoderm is nearly twice as thick as in other parts. A linear demarcation appears in the midst of this thickened layer (fig. 4); and at the same time indications of a separation are traceable between the distal extremity of the thickened portion and the rest of the blastoderm: it is as if the latter were giving way at this point. In some specimens the cell-cavities of the inner portion of the thickening were particularly well marked; and the coarsely granular central substance exhibited a tendency to break up into large globular masses, which became particularly distinct on the addition of water.

It is in the largest of these germs that the resemblance of the pseudovum to an ovum is completed by the formation of a pseudo-vitelline membrane (fig. 3, *a*). This structureless homogeneous membrane is, doubtless, developed by a process of excretion, either from the pseudovum or from the walls of the chamber which contains it. It completely envelopes the pseudovum, and acquires greater thickness and strength as development proceeds.

The embryo first becomes clearly fashioned in pseudova between $\frac{1}{200}$th and $\frac{1}{150}$th of an inch in length (Pl. XXXVII. [Plate 2] fig. 5). At the distal extremity, in the region of the thickening of the blastoderm, the latter appears separated into two portions, the outer of which forms a sort of hood over the inner. The hood eventually becomes the hinder part, if not the whole, of the abdomen of the larva. It is continuous, on the side answering to the dorsal side of the larva, with the rest of the blastoderm, which now, instead of enclosing the pseudovitellus, lies partly beneath and partly behind it. That portion of the blastoderm which lies behind the pseudovitellus, and parallel with the hood, is the rudiment of the sternal region of the thorax; and I shall hereafter term it the thoracic segment of the blastoderm. That part of the blastoderm which lies beneath the pseudovitellus will become the sternal region of the head; and I shall therefore call it the cephalic segment, while the hood itself is the abdominal segment of the blastoderm.

The thoracic segment, it will be observed, is in this stage bent up at right angles to the axis, and reaches the dorsal region, which it bounds posteriorly. The cephalic segment, on the other hand, hardly extends upwards at all, but lies in one plane; so that the anterior end of the embryo is almost wholly formed by the pseudovitellus. The latter is aggregated into a few large globular masses, which are in immediate contact with the pseudovitelline membrane on their dorsal surface.

The pseudovitellus is in immediate contact inferiorly with a layer

of the blastoderm of a more pellucid aspect than the rest, and separated from it by a more or less distinct line of demarcation. This layer (*q*) could be detected only on the dorsal face of the thoracic and cephalic segments, and owed its superior transparency to the comparatively large size of the clear cavities surrounding its endoplasts.

That portion of the layer which covered the posterior portion of the thoracic segment was particularly remarkable for the size and clearness of its cells and their endoplasts (*r*). In the progress of development, the central portion of the alimentary canal occupies a place nearly corresponding to the centre of the clear layer; while, if we trace out the site of the rest of the mass in larger and larger embryos (Pl. XXXVIII. [Plate 3] figs. 1, 3, 4, 5), we find it always retaining the same relative position to the reflected abdominal hood, but gradually enlarging, and eventually becoming subdivided into five oval lobes upon each side, each of which surrounds itself with a membrane, and assumes the form of the terminal chamber of one of the pseudovarial cæca. It would be a great mistake to suppose that it is only one of these chambers, however; it is in fact the rudiment of an entire cæcum; and before the embryo leaves the parent, it becomes divided into three chambers by the gradual development and metamorphosis of pseudova in the way described above.

The granular pseudovitellus takes no part whatever in the formation of the reproductive organs. In embryos of $\frac{1}{94}$th of an inch in length, I could very plainly observe a clear space with an endoplast in the middle of each of its spheroidal masses (Pl. XXXVIII. [Plate 3] fig. 3). Similar masses constitute a larger or smaller proportion of the corpus adiposum of the larva and adult insect; and I believe that the latter proceeds from the former.

§ 5. *Summary and Comparison of Germs and Ova*

I will now sum up the results of the observations which have been detailed in the preceding pages.

1. The pseudovarium consists of vagina, oviducts, and pseudovarian cæca.

2. The vagina is unprovided with either spermatheca or colleterial glands.

3. The pseudovarian cæca are each divided into many chambers by constrictions.

4. The apical chamber contains bodies which are not distinguishable from the germinal vesicles and spots of the true ovaria.

5. These bodies, surrounded by a mass of clear substance repre-

senting a yelk, are set free as pseudova, and are then undistinguishable from true ova.

6. The pseudova are eventually converted into cellular germs, apparently by the same process as that by which an ovum is converted into an embryo.

7. In these germs the central part becomes a granular pseudovitellus, the peripheral a blastoderm ; the rudiments of the different organs next appear, and the germ becomes surrounded by a pseudovitelline membrane.

8. Eventually the pseudovitellus probably becomes the corpus adiposum.

9. All the other organs are developed from the blastoderm, which becomes distinguished into two layers. From the outer of these the muscles, nerves, limbs, and tegument are developed, while the inner gives rise to a part of the alimentary canal (?) and to the reproductive organs or pseudovarium of the larva.

10. The pseudovarium contains no particle of unchanged tissue of the germ, but is a considerably differentiated and readily distinguishable mass. The mass divides into ten lobes anteriorly ; and these lobes become the pseudovarian cæca. Before the larva is born, each cæcum is divided into three chambers, the two posterior of which contain rudimentary embryos.

11. The genital apparatus of the oviparous female consists of a vagina, oviducts, and ovarian cæca. The latter are multilocular ; and the vagina is provided with the spermatheca, and the two colleterial glands first demonstrated by Von Siebold.

12. The rudiments of the ova are undistinguishable from those of the pseudova. They are developed in the lower part of the apical ovarian chamber, the upper part of which is occupied by the bodies I have termed ovarian glands. The ova are not at first enveloped in a chorion.

13. In the lowest chamber the ova are provided with a chorion, vitelline membrane, and what appears to be a micropyle.

If these propositions are correct, I see no valid objection to the conclusion, that the agamic offspring of *Aphis* is developed from a body of precisely the same character as that which gives rise to the true egg. The pseudovum is detached from the pseudovarium in the same way as the ovum from the ovarium. In both cases, the act of separation is in every respect a process of gemmation.

From this point onwards, however, the fate of the pseudovum is different from that of the ovum. The former begins at once to be converted into the germ ; the latter accumulates yelk-substance, and

changes but little. Both bodies acquire their membranous investment rather late; within it the pseudovum becomes a living larva while the ovum is impregnated, laid, and remains in a state of rest for a longer or shorter period.

Although, then, the pseudovum and the ovum of *Aphis* are exceedingly similar in structure for some time after they have passed out of the condition of indifferent tissue, it cannot be said that the sole difference between them is, that the one requires fecundation and the other not. When the ovum is of the size of a pseudovum which is about to develop into an embryo, and therefore long before fecundation, it manifests its inherent physiological distinctness by becoming, not an embryo, but an ovum. Up to this period the influence of fecundation has not been felt; and the production of ova instead of pseudova must depend upon a something impressed upon the constitution of the parent before it was brought forth by its viviparous progenetrix.

In this respect, the ova of *Aphis* exhibit the same relation to the pseudova as the ephippial eggs of *Daphnia* (whose development has been so well described by Mr. Lubbock) bear to the agamic eggs; for the histological change in the ovarium of *Daphnia*, which precedes the development of the ephippial eggs, is clearly shown by Mr. Lubbock to have no relation to fecundation.

Let me remark on yet another interesting, though perhaps only partial, analogy. Von Siebold has shown that the ova of the Queen bee produce females or males, according as they are fecundated or not. The fecundated ovum produces a queen or a neuter according to the food of the larva and the other conditions to which it is subjected; the unfecundated ovum produces a drone. Now, what have we seen in *Aphis*? The fecundated egg produces viviparous *Aphides*, which are the equivalents of the neuter bees; and from them are eventually produced males and oviparous females. The oviparous females are fecundated and lay eggs which produce only viviparous or neuter *Aphides*.

On the view which Dr. Carpenter and myself take of the zoological individual, the whole produce of a single fecundated ovum of the *Aphis* is as much the *Aphis* individual as it is the Bee individual. Consequently we have two equivalent and related series.

I.		II.		
Bee. Impregnated ova	producing	Neuters or females	producing	Ova requiring impregnation, and males. Females which give rise to ova requiring impregnation, and males.
Aphis. Impregnated ova		Viviparous neuters		

The fact that in the one case the males are developed from pseudova resembling fully-formed true ova, and in the other from pseudova resembling imperfectly-formed ova, makes no essential difference in the analogy, but only demonstrates still more clearly the impossibility of drawing any absolute line of demarcation histologically between ova and buds.

§ 6. *Hypothetical Explanations of Agamogenesis*

The majority of writers on the wonderful phenomena of Aphidian life have been content to state the facts more or less clearly; but Morren, who has done this so clearly and philosophically, has in addition carelessly thrown out a hint of a mode of explaining them. The agamic *Aphis*, he says, is a portion of organized tissue which individualizes itself:—

"Suppose that vitality is sufficiently energetic to impress, on the tissue which individualizes itself, the form of the producing species, and you have the generation of the *Aphides*. This energy becomes lost at the end of a certain number of generations, and a new impulse becomes necessary. It is that of the male. In my youth I might have adopted with pleasure such an hypothesis as this; but now I prefer to doubt: the facts which I have set forth are worth more than a theory."

The hypothesis is, however, to my mind, in no essential particular distinguishable from that hypothetical explanation which has been propounded by the author of the well-known work on "Parthenogenesis." Substitute for "energy of the male," in the foregoing passage, "spermatic force;" and the difference between the two hypotheses becomes evanescent.

But this is a question of minor importance as compared with the value of the hypothesis in itself; and it is with regard to this latter point that I now propose to make a few remarks.

Professor Owen's views are, I believe, fairly stated in the following extracts from the work cited:—

"We find derivative germ-cells, and masses of nuclei like those resulting from the final subdivision of germ-cells, retained unchanged at the filamentary extremities of the branched uterus forming the ovaria of the larval Aphides."—*l. c.* pp. 7, 8.

"According to my own observations, the germs are perceptible in the embryo Aphis, above the simple digestive sac, before any organs have been formed for their reception. And with regard to the nature of the organs when formed, I may remark that the continuity of

the ovarian tubes with the oviducts in all insects, is such as to render the negation of the term 'ovary' to those two bodies from which the slender extremities of the eight oviducal and uterine tubes proceed in the larval Aphis, to say the least, quite arbitrary. My examinations agree with those of Siebold, in determining scarcely any appreciable difference between the ovaria of the oviparous and those of the viviparous females. The contents of the ovarian tubes differ, inasmuch as they contain oval masses of granules or nuclei, comparable to the germ-mass in its state of minutest subdivision, in the virgin Aphides, and not ova with the germinal vesicle as in the oviparous females." —*Ibid.* p. 38.

"The completion of an embryonic or larval form by the development of an ovarian germ-cell, or germ-mass, as in the Aphis, without the immediate reception of fresh spermatic force, has never been known to occur in any vertebrate animal.

"The condition which renders this seemingly strange and mysterious generation of an embryo without precedent coitus possible, is the retention of a portion of the germ-mass unchanged. One sees such portion of the germ-mass taken into the semitransparent body of the embryo Aphis, like the remnant of the yelk in the chick. I at first thought that it was about to be enclosed within the alimentary canal, but it is not so. As the embryo grows, it assumes the position of the ovarium, and becomes divided into oval masses and enclosed by the filamentary extremities of the eight oviducts. . . . ."—*Ibid.* pp. 69–70.

"It would be needless to multiply the illustrations of the essential condition of these phenomena. That condition is, the retention of certain of the progeny of the primary impregnated germ-cell, or, in other words, of the germ-mass unchanged, in the body of the first individual developed from that germ-mass, with so much of the spermatic force inherited by the retained germ-cells from the parent cell or germ-vesicle as suffices to set on foot and maintain the same series of formative actions as those which constituted the individual containing them."—*Ibid.* p. 72.

"The physiologist congratulates himself with justice when he has been able to pass from cause to cause, until he arrives at the union of the spermatozoon with the germinal vesicle as the essential condition of development—a cause ready to operate when favourable circumstances concur, and without which cause these circumstances would have no effect.

"What I have endeavoured to do has been to point out the conditions which bring about the presence of the same essential cause in

the cases of the development of an embryo from a parent that has not itself been impregnated. The cause is the same in kind, though not in degree, and every successive generation, or series of spontaneous fissions, of the primary impregnated germ-cell, must weaken the spermatic force transmitted to such successive generations of cells.

"The force is exhausted in proportion to the complexity and living powers of the organism developed from the primary germ-cell and germ-mass."—*Ibid.* pp. 72, 73.

These statements are repeated in the recently published second edition of Professor Owen's "Lectures on the Invertebrata."

The paragraphs I have cited contain two kinds of propositions—assertions with respect to matters of fact, and deductions from those assertions. The former are, according to my observations, incorrect; and, as I conceive, the latter are unfounded.

As regards the first citation, for instance, the contents of the apical chambers of the pseudovaria are *not* by any means identical with those "resulting from the final subdivision of germ-cells retained unchanged," as the most cursory comparison of the two structures will show.

In the second citation it is affirmed that the germs are perceptible in the embryo before any organs are formed for their reception. This, again, is an error if my observations are correct. The absence of figures, and the too vague and general character of the descriptions in Professor Owen's work, render it very difficult to understand what he really has seen; but I imagine that he has taken the substance which constitutes the rudiment of the whole pseudovarium, and which becomes differentiated partly into pseudova, partly into the walls of the organ, for a mass of germs. What is meant by "those two bodies from which the slender extremities of the eight oviducal and uterine tubes proceed," and which are supposed to be ovaries, I am at a loss to divine. There are no such bodies, that I can discover.

In the latter part of the same citation, the existence of a histological difference between the contents of the pseudovarium and those of the ovarium is asserted. But there is assuredly nothing in the former to which the description can apply; and I re-affirm the impossibility of drawing any histological line of demarcation between the pseudova and the young true ova.

How any one who carefully studies the development of *Aphis* can arrive at the conclusion that a portion of the germ-mass is taken into the body of the embryo *Aphis*, "like the remnant of the yelk of the chick," I know not; and, for the reasons mentioned above, I even doubt if I clearly apprehend what is meant. Dr. Burnett (*l. c.* p. 73)

assumes that what is intended by "portion of the germ-mass" is what I have termed the pseudovitellus. In that case the statement is erroneous; for the pseudovitellus takes no share in the formation of the pseudovarium. If, on the other hand, the true rudiment of the pseudovarium is indicated, the statement in question is equally incorrect; for this is never out of the body, and hence can hardly be taken into it, nor can that out of which the so-called "oviducts" are produced be properly said to become "connected with them," or to "aid in forming their filamentary extremities."

When the basis of a hypothesis is shown to be incorrect, the hypothesis itself is commonly considered to be disposed of; but possibly in the present case it may be urged that, although the contents of the pseudovarium *are* wholly dissimilar "to the germ-mass in its state of minutest subdivision," they are nevertheless so little changed that my criticism of the phrase is trivial. To this I reply that, whether the alteration be small or great, it is *as* great as that which occurs in the terminal cæca of a gland, or in a true ovarium, and that the tissue of the apical pseudovarian chamber is far more differentiated than the indifferent tissue which constitutes the youngest portion of an ordinary epithelium or epidermis.

Whatever conclusions are based upon the resemblance of the tissue of the pseudovarium to that of the embryo, must therefore apply in equal or greater force to the tissues which I have just named; and, unless reason can be shown to the contrary, whatever powers are possessed by the one, in virtue of this similarity, must be possessed in equal or greater degree by the other.

But in this case what becomes of the hypothetical explanation of the asexual reproduction of *Aphis*, under discussion?

The condition of such reproduction is, according to the hypothesis, the retention of "certain of the progeny of the primary impregnated germ-cell unchanged," "with so much of the spermatic force, inherited by the retained germ-cells from the parent-cell or germ-vesicle, as suffices to set on foot and maintain the same series of formative actions as those which constituted the individual containing them."

Let us imagine, for the sake of argument, that the amount of histological change in the pseudovarian mass is unimportant. I am ready to suppose even, in accordance with the hypothesis, that its cells retain sufficient "spermatic force" (whatever that may be) to commence an independent life. But I ask, how does this explain agamogenesis? Why does not the epithelium of the ovarium (which is as little or less changed) give rise to young without impregnation? Why are not the young cells of glands, which are as little changed

"parthenogenetic"? Why, finally, does not the deep substance of our epidermis and epithelium, which absolutely more nearly resembles embryonic tissue than the structure of the pseudovarium does, give rise to young?

It may be replied, however, that the supposed "spermatic force" is exhausted by the repeated subdivisions of the germ-cell before it becomes a part of the deep epidermic tissue; for it is one condition of the hypothesis, that every successive generation or series of spontaneous fissions of the primary impregnated germ-cell must weaken the "spermatic force" transmitted to such successive generation of cells.

I presume, however, that the original "spermatic force" is at least as strong in a Man as in an *Aphis.* The average size of the embryo-cells in *Aphis* is at least not greater than in Man, and the specific gravities of their essential tissues are not very different; so that we may fairly assume that as many embryo-cells go to form a given mass of *Aphis* as of Man. In that case the impregnated embryo-cell must subdivide as often; and therefore the "spermatic force" must become as much exhausted in forming, say, a grain or a pound of *Aphis*, as in giving rise to the like quantity of human substance.

In his Lectures, Professor Owen adopts the calculations taken by Morren (as acknowledged by him) from Tougard, that a single impregnated ovum of *Aphis* may give rise, without fecundation, to a quintillion of *Aphides.*[1] I will assume that an *Aphis* weighs $\frac{1}{1000}$th of a grain, which is certainly vastly under the mark. A quintillion of *Aphides* will, on this estimate, weigh a quatrillion of grains.

He is a very stout man who weighs two million grains; consequently the tenth brood alone, if all its members survive the perils to which they are exposed, contains more substance than 500,000,000 stout men—to say the least, more than the whole population of China! And if the law cited above be correct, the "spermatic force" in each cell of an *Aphis* of this brood must be diminished 500,000,000 times as much as that of a single human cell; nevertheless the "spermatic force" of the *Aphis* cell is enough to impel it to the production of young, while that of the human cell is not!

When to these considerations I add, that it has been shown that the agamic propagation of the *Aphis* may, under proper conditions, be continued for four years without interruption, in which case the "spermatic force" in the later broods must stand in an infinitely minute ratio even to that contained in the cells of the tenth genera-

[1] I have not thought it worth while to add, in the products of the generations preceding the tenth.

tion, the *reductio ad absurdum* by simple arithmetic, of the so-called explanation, appears to me to be sufficiently obvious.

For the sake of argument, however, I am willing still to suppose for a moment that agamogenesis does take place in consequence of the retention of a "spermatic force." But I must ask, how does this phrase constitute an explanation of the phenomena? Nothing is more common than the misuse of the word "force" on the part of those who are more versed in the phraseology, than trained in the severe methods, of physical science. The impatient inquirer every now and then calls in the aid of molecular force, or chemical force, or magnetic force, or od-force, to account for the existence of a mass of phenomena which will not arrange themselves under any of his established categories—forgetting that a "force," the conditions of whose operation (that is, whose laws) are undetermined, is but a scientific idol, at once empty and mischievous,—empty, because it is but a phrase without real meaning; mischievous, because it acts as an intellectual opiate, confusedly satisfying many minds and obstructing the progress of inquiry into the real laws of the phenomena. If we show that a fact is a case of a law, we explain that fact; but explanation by reference to an undefined "force," of questionable existence, is simply 'ignorance writ large.'

Now, how does the hypothesis fulfil the indispensable conditions of a genuine explanation? In the first place, what proof is there of the existence of such a force as 'spermatic force'? All that we *know* is, that an ordinary ovum will not undergo those changes which constitute development without the contact of the spermatozoon. Hence it is concluded that some force contained in the spermatozoon is the efficient cause of all these changes. But what would be thought of the artillerist who should imagine he had explained the propulsion of a bullet by saying it was 'trigger force'? Or, to take an illustration from phenomena of a like order to those under discussion: a seed will not grow unless it is exposed to a certain amount of warmth and moisture; but have I explained the growth by saying that it is the effect of 'heat and moisture force' which becomes diffused through the seed?

The very existence of this "spermatic force," then, is a gratuitous assumption; and if we seek for its laws of action, we find but two stated: first, that it becomes weakened by the successive divisions of the germ-cell; second, that "the force is exhausted in proportion to the complexity and living powers of the organism developed from the primary germ-cell and germ-mass."

I have shown to what singular consequences the first assumption

leads us; it remains only to consider the second. If it be true, the occurrence of agamogenesis in the animal kingdom must bear an approximatively inverse ratio to the complexity of the organization of the different groups. Let us examine one or two sub-kingdoms in this point of view. Among the *Annulosa*, the *Rotifera* and *Turbellaria* possibly possess it to a small extent; the *Nematoidea* do not possess it at all. Many *Trematoda* possess it; others, such as *Aspidogaster*, have nothing of the kind. The *Acanthocephala* are not known to possess it; the *Echinodermata* are regarded by Professor Owen as possessing it, but their different families show every gradation from simple metamorphosis to something like agamogenesis. A few *Annelida* possess the power in a marked degree; in many, nothing of the kind is known. The *Nais* has it; the Earth-worm and the Leech have it not. Of the *Crustacea*, some, such as many *Branchiopoda*, exhibit it in the highest perfection; but no trace of it has yet been found in *Copepoda*, *Cirripedia*, *Pœcilopoda*, *Edriophthalmia*, or *Podophthalmia*. In the *Myriapoda* and *Arachnida* the process is not known: but we find it in the highest *Articulata*—the *Insecta*—and this not, so far as we know at present, in *Aptera* or *Orthoptera*, but in a few *Hemiptera*, *Hymenoptera* and *Lepidoptera*; and there is every reason to believe that it only occurs in isolated, though perhaps in many, genera of these orders. Take the *Mollusca* again: agamogenesis occurs in the *Polyzoa* and *Ascidioida*, not in the *Brachiopoda*. It is not known to occur in any of the *Lamellibranchiata*; and among the higher *Mollusca* the nearest approach to it is presented by the animal (whatever it is) which gives rise to the "Synapta-schnecken" (high Gasteropods), and by the Hectocotyligenous *Cephalopoda*.

After this simple statement of well-known facts, I need not remind even the tyro in zoology, that there is no evidence of an inverse relation between the occurrence of agamogenesis and complexity of organization.

I have hitherto, in the course of this argument, confined myself in the main to the development of *Aphis*; but it is only just to observe that the author of the hypothesis brings forward yet another original observation in support of his large generalization:—

"In the freshwater polype, the progeny of the primary impregnated germ-cell retained unaltered in that body, may set up, under favourable stimuli of light, heat, and nutriment, the same actions as those to which they owed their own origin; certain of the nucleated cells do set up such actions, those, *e.g.* in the *Hydra fusca*, which are aggregated near the adhering pedicle or foot; and the result of their increase by assimilation and multiplication is, to push out the contiguous integu-

ment in the form of a bud, which becomes the seat of the subsequent processes of growth and development; a clear cavity or centre of assimilation is first formed, which soon opens into the stomach of the parent; but the communication is afterwards closed, and the young hydra is ultimately cast off from the surface of the parent."[1]—'Lectures,' 2nd ed., p. 124.

I have had occasion carefully to watch the process of gemmation not only in *Hydra*, but in many species of all the other subdivisions of the *Hydrozoa*; and I venture to assert that no such process as that described by Professor Owen takes place in any one of them.

The bud is from the first in communication with the cavity of the body, of which it is a mere diverticulum, whose walls are a little thickened at the extremity. No special cell or group of cells can be discovered as the centres whence growth proceeds. No "integument" is pushed out by any thing beneath it; but the outer layer of the body of the animal thickens and grows *pari passu* with the growth of the bud. No especial accumulation of derivative germ-cells can be seen in any part of the body of any *Hydrozoon*; and before gemmation commences there is no distinguishable difference of texture between the part in which gemmation commences and any other portion of the body. Furthermore, if a complex Hydrozoon, such as a *Physophora* or *Agalma*, be examined, it will be found that there is no histological distinction whatsoever between that part of the body which is to give rise to a free swimming generative zooid, and that which produces merely a bract, a tentacle, or a stomach.

In this case, then, as in that of the *Aphis*, the hypothesis receives no support from, but is totally opposed by, facts; and I unreservedly adopt the conclusion (long since clearly and well expressed by Dr. Carpenter), that "spermatic force" is but a name without definite meaning, applied to that which is not proven to exist, and the assumption of whose existence, even, does not help us a single step towards the understanding of the wonderful phenonema of agamogenesis.

Truly we may say, with Degeer (*l. c.* p. 129), "Les Pucerons sont des insectes bien capables de déranger tout système formé de génération, et de mettre en déroute tous ceux qui s'efforcent d'expliquer ce mystère de la nature."

But the question may be asked: if the "spermatic force" be a myth, what *is* the cause of the phenomena? Considering that the groundwork of modern physiology is not a score of years old, I do

[1] I have cited this passage from the 'Lectures' rather than from the work on "Parthenogenesis," as they may be supposed to contain the expression of the author's latest views.

not think the confession of our inability to answer that question at present is any opprobrium to science.

When we know why, in a mass of tissue of identical structure throughout, one part becomes a brain, and another a heart, and a third a liver—when we can answer these every-day questions of the sphinx, we may attempt her more difficult riddles without running too great a risk of being devoured.

At the present time it seems to me well nigh hopeless to look for an explanation of these phenomena. Some such classification of them, however, as will indicate their analogies with other vital manifestations, may fairly be attempted, and, when successfully carried out, will prove the first step towards an explanation.

§ 7. *Classification of the Phenomena of Agamogenesis*

It does not seem to be very difficult to effect such a classification. In the course of the development of the total product of a single impregnated ovum (which, with Dr. Carpenter, I regard as the zoological individual), one of two things may occur: either all the living products may remain in connexion with one another, or they may become separated from one another. The former case I term *Continuous*, the latter *Discontinuous Development.*

In continuous development, the size may increase, the form and texture remaining unchanged—constituting simple *growth*; or, the size remaining unchanged, the form and texture may alter—constituting simple *metamorphosis*; or the two processes may be combined, as in all those changes which we term *gemmation*, without separation from the parent.

Discontinuous development differs from continuous only in this, that the products of the growth and metamorphosis of the embryo become separated into two or more portions, which, when they retain their vitality independently, are termed "zooids."

When the produced "zooid" is capable of development into an independent organism without the influence of an act of conjugation with another zooid, I term the process *agamogenesis.* The producing zooid may be devoid of sexual organs, as in the *Salpæ*, many *Hydrozoa*, many *Trematoda*—in fact, in the great majority of cases of agamogenesis.

I term the first producing zooid of the individual the *protozooid*; the produced zooids, *deuterozooids.* In some cases the deuterozooids acquire sexual organs, and give rise to ova and spermatozoa; but in others they produce new zooids: thus broods of *tritozooids*, &c., will

be produced. When the producing or protozooid possesses no sexual organs, I think Professor Owen's term of "*metagenesis*" might well be applied to the kind of agamogenesis; but where the protozooid possesses sexual organs, and its buds have all the histological characters of ova, then the process may fairly enough be termed *parthenogenesis*.

Finally, the produced zooid may be incapable of development into an independent organism, unless it conjugate with another zooid. In this case we have sexual reproduction, or *gamogenesis*.

The natural character of this classification of the various modes of development is manifest when it is thrown into a tabular form:—

Development.	Continuous		Growth.
			Metamorphosis.
			Gemmation without fission.
	Discontinuous. (Gemmation with fission).	Agamogenesis.	Metagenesis.
			Parthenogenesis.
		Gamogenesis.	

Whatever hypothesis we may entertain with respect to the nature of these processes, and however we may think fit to conceive the nature of the "individual," I think it must be admitted, that all the phenomena of development in the animal kingdom (and I would venture to add in the vegetable kingdom also) fall under one or other of these heads.

Furthermore, all these modes of development pass into one another. Growth and metamorphosis are combined in all animals. Gemmation, so long as the gemma continues attached, is but a peculiar kind of growth and metamorphosis. From the fixed bud to the separate one, we have all gradations; and fission is little more than a peculiar mode of budding.

Free gemmation is "metagenesis" when the bud is not developed within the homologues of the sexual reproductive organs; it becomes "parthenogenesis" when the bud is developed within such organs; finally, when the free bud requires conjugation with another free bud for its development, we have gamogenesis, or sexual reproduction: but cases such as those of *Daphnia* and *Apis* show that the histological element, which is at one time agamogenetic, may at another be gamogenetic.

Time was when the difficulty of the physiologist lay in understanding reproduction without the sexual process. At the present

day, it seems to me that the problem is reversed, and that the question before us is, why is sexual union necessary? Far from seeking for an explanation of the phenomena of gemmation in the transmitted influence of the spermatozoon, the philosopher acquainted with the existing state of science will seek, in the laws which govern gemmation, for an explanation of the spermatic influence.

PART II

Read January 21st, 1858.

§ 1. Embryogeny of the external organs of *Aphis*—§ 2. Embryogeny of *Mysis* as exemplifying the *Crustacea*—§ 3. Embryogeny of *Scorpio* as exemplifying the *Arachnida*—§ 4. Generalizations regarding the Embryogeny of the *Articulata*, and Morphological Laws based on them—§ 5. The Embryogeny of *Articulata*, *Mollusca* and *Vertebrata* compared.

§ 1. *Embryogeny of the external organs of* Aphis

IN the previous part of this paper I sketched so much of the development of the embryo of *Aphis* as was indispensable to the clear understanding of its reproductive processes; but it appears to me that the bearings of the embryogeny of this Insect upon morphology render it worthy of a more attentive and detailed consideration.

It would be well worth while, indeed, to trace out the development of all the organs of this remarkable animal; but as I shall have for some months no leisure for labours involving so great an expenditure of time, I will content myself for the present with a notice of some of the leading features presented by the development of the external organs.

I have already stated that one of the earliest changes in the germ of the young of the viviparous *Aphis* is the differentiation of its cellular mass into a central portion, which takes on the appearance and functions of a yelk, and which I termed "the pseudovitellus," and a peripheral coat or layer, the blastoderm. The blastoderm next becomes thickened posteriorly; and in this thickening a division takes place from without inwards, so that it is separated into a posterior flap and an anterior portion, which are only continuous dorsally. It is the flap which is the rudiment of the abdomen, while that portion of the blastoderm against which it is folded stands in the same relation to the thorax. In front of this is the rudiment of the head, constituting by far the largest portion of the blastoderm.

Dorsally and posteriorly, the rudiment of the head is originally continuous with the thoracico-abdominal thickening; but a separation early takes place at this part, and the interval is occupied by the pseudovitellus, which here comes into immediate contact with the pseudovitelline membrane.

In an embryo $\frac{1}{100}$th of an inch in length (Pl. XXXVII. [Plate 2] fig. 5), this interval has increased so much, that the cephalic blastoderm does not extend on to the dorsal region at all, but lies almost flat under the pseudovitellus, in the anterior half of the ventral region.

In embryos $\frac{1}{110}$th of an inch in length (Pl. XXXVII. [Plate 2] fig. 6), I have found the cephalic portion of the blastoderm beginning to extend upwards again over the anterior face of the germ, so as to constitute its anterior and a small part of its superior wall.

This portion is divided by a median fissure into two lobes, which play an important part in the development of the head, and will be termed the "procephalic lobes." I have already[1] made use of this term for the corresponding parts in the embryos of *Crustacea*.

The rudimentary thorax presents traces of a division into three segments; and the dorso-lateral margins of the cephalic blastoderm, behind the procephalic lobes, have a sinuous margin.

It is in embryos between this and $\frac{1}{100}$th of an inch in length that the rudiments of the appendages make their appearance; and by the growth of the cephalic, thoracic, and abdominal blastoderm, curious changes are effected in the relative position of these regions.

In embryos about $\frac{1}{100}$th of an inch in length (Pl. XXXVIII. [Plate 3] fig. 1, 1*a*), the procephalic lobes are so completely bent backwards as to lie close against the tergal surface of the rest of the cephalic blastoderm, so that no pseudovitelline granules can any more be seen in this region of the body. At the same time the lobes have enlarged, and extend back as far as the base of the fourth pair of visible cephalic appendages. Their infero-lateral angles are rounded and produced, forming an elevation which appears to be the rudiment of the eye.

Below the anterior extremity of the embryo, the blastoderm is produced on the median line into a tongue-like process (*lb*), whose inferior part eventually becomes the labrum, while superiorly it sends a triangular process (the rudiment of the clypeus) into the interval between the procephalic lobes.

Immediately behind the labrum, the blastoderm curves at first

[1] 'Lectures on General Natural History,' Med. Times and Gazette, 1856-7.

downwards, and then sharply upwards and backwards, to a little beyond the line of the posterior edge of the procephalic lobes.

The whole of this portion of the blastoderm belongs to the head. In the re-entering angle between it and the labrum the mouth is placed; it is a small aperture, whence the œsophagus can be traced ascending and passing backwards with a gradual curve.

Behind the cephalic region, the thoracic blastoderm passes nearly horizontally backwards, and already presents traces of a division into its three somites. Its upper surface is close to the pseudovitelline membrane, and consequently is covered by but a very thin layer of yelk-like granules.

At the end of the rudimentary thorax the blastoderm is suddenly folded forwards, so that the sternal surface of the hinder part of the future abdomen is almost in contact with that of the thorax. Having come opposite the anterior edge of the thorax, it is bent backwards, at right angles to its previous direction, for a short distance,—the extreme end being finally folded parallel with this part, and with its apex towards the head.

The great mass of the yelk lies over the abdominal blastoderm, in the space left between it and the pseudovitelline membrane. The appendages present a singular and beautiful uniformity. No trace of the pigment of the eyes is to be seen. The next anterior pair of appendages (*a t*) are more slender and elongated than the others, and are bent inwards near their base so as to form a sort of elbow. In consequence of this, their terminal portions are more approximated than their distal ones, and lie close together and parallel. These appendages are the antennæ; and it is worthy of remark, that they arise from the procephalic lobes, or from the point of junction between them and the rest of the cephalic blastoderm above the mouth.

Behind these and behind the mouth (though the anterior pair are very close to that aperture, and might even be described as more or less lateral in relation to it) are three pair of short, similar, conical processes. Of these the anterior pair (IV′) are the largest, and are the mandibles; the two other pairs are nearly equal: the anterior (V′) represent what are ordinarily termed the maxillæ, but which might be more properly called "first maxillæ," since the second pair (VI′), which eventually give rise to the so-called "labium," are precisely like them, and, as Zaddach (*l. c. infra*) has shown, fully deserve the title of "second maxillæ."

Three pairs (VII′, VIII′, IX′) of short processes, unjointed and not much longer than the trophi, represent the thoracic limbs.

The abdomen presents obscure traces of a division into segments.

In an embryo $\frac{1}{95}$th of an inch in length (Pl. XXXVIII. [Plate 3] fig. 1, 1*a*, and 2), the procephalic lobes have extended so far back as completely to cover the tergal region of the head, and even to pass a little beyond the line of the last maxilla posteriorly. The fold or depression separating the thorax from the head has become deeper; the antennæ have greatly elongated, and are bent downwards and inwards, so as to meet in the middle line below, and cover the mandibles.

The first maxillæ are larger than the mandibles, and somewhat expanded at their extremities. The second maxillæ are more slender; and their bases are in a line with those of the mandibles, while those of the first maxillæ have taken a more external position. Consequently, the bases of the trophi, instead of forming two nearly parallel rows as at first, are now arranged as a hexagon, whose outer angles are constituted by the first maxillæ.

The thoracic members have greatly elongated, the hinder pair being the longest.

In embryos $\frac{1}{70}$th of an inch in length (Pl. XXXVIII. [Plate 3] fig. 5), the blastoderm is found to have undergone a wonderful change. Instead of being folded upon itself ventrally by the flexure of the abdomen against the thorax, it has become completely extended; and so thoroughly has this extension taken place, that the abdomen is now convex inferiorly. At the same time the blastoderm has grown upwards over the sides of the body, and roofs-in its tergal region. The head is closed by the union of the procephalic lobes, and is now, in consequence of the increased length of the body, proportionally much smaller. The pigment of the eyes appears in a few scattered granules towards the posterior margin of the head on each side.

If the appendages be examined as they become metamorphosed in a succession of specimens intermediate in size between $\frac{1}{100}$th and $\frac{1}{70}$th of an inch, the antennæ are found gradually to increase in length and to become jointed. The growth of the mandibles and first maxillæ in length, on the contrary, is suspended; and they remain as short thick tubercles (Pl. XXXIX. [Plate 4] fig. 2), from whose inner surface a long chitinous filament gradually arises. These filaments, thickening and elongating, become the blades of the mandibles and maxillæ. The growth of the second maxillæ makes up, by its excess, for the arrest of development of the mandibles and first maxillæ; for having already approximated, their confluent or connate bases elongate as one great process, which extends back in the middle line between the thoracic legs, until at length it attains

more than half the length of the body, and constitutes the well-known proboscidi form "labium" of the *Aphis*.[1]

The thoracic members or legs have elongated so much, that their terminations are bent inwards, to allow of their lying within the pseudovitelline membrane. Their characteristic subdivisions are indicated; and the terminal claws are beginning to be formed.

From this size up to that at which the larvæ are born (Pl. XXXIX. [Plate 4] fig. 4) (when they are less than $\frac{1}{40}$th of an inch in length), the principal changes are the following:—The appendages as compared to the body, and the latter as compared to the head, undergo great elongation. The anterior pair of thoracic limbs and its somite, the prothorax, come into very close contact with the head, so that the cervical separation becomes obsolete, or is only indicated by a groove. The labrum and labium acquire their characteristic form and proportions; and the mandibular and maxillary setæ elongate, and take their final position.

The "siphons," so characteristic of the genus, appear as obtuse tubercles on the dorso-lateral region of the fifth abdominal somite. The little larva exhibits unequivocal signs of life, but still remains enclosed within its pseudovitelline membrane, to which another transparent and structureless envelope, fitting the body of the larva and all its limbs as a loose glove fits the hand, seems to have added itself. This second coat is, in fact, the embryonic integument, which is now being cast; so that the creature must undergo its first ecdysis either before, or immediately after, it is born. The head assumes its normal proportions. The corneæ become facetted; and the pigment increases greatly in amount, assuming the form of an oval deep-red patch. The clypeus and the procephalic lobes unite, but readily give way when the head is crushed, and allow of the exit of the cerebral mass, which has in the meanwhile been produced by a differentiation of the inner substance of the procephalic lobes, just as the other ganglia are the product of the blastoderm of their somites.

If the account of the development of the external organs of *Aphis* which I have just given be compared with the statements of Kölliker[2] and Zaddach,[3] it will be found that there is a close correspondence in all essential respects between the embryogenic phenomena of at least three orders of *Insecta*—the *Hemiptera*, the *Diptera*, and the

[1] Zaddach considers, from his observations on *Phryganea* and other Insects, that the labium is the product, not of confluent maxillæ, but of an outgrowth of the sternum by which these are supported, the maxillæ remaining as the labial palpi. I do not deny that this may be the case in *Aphis*; but I have been unable to find positive evidence of the fact.

[2] De prima Insectorum Genesi, 1842.

[3] Die Entwickelung des Phryganiden-Eies, 1856.

Neuroptera. And, considering the universality of the law that the embryogenic processes of members of the same class have a similar fundamental character, I do not doubt that the development of all insects is, in its main features, a process similar to that described in *Aphis.*

§ 2. *Embryogeny of* Mysis *as exemplifying the* Crustacea.

But more than this, if we extend our researches into the embryogeny of the other two principal[1] classes of the *Articulata*, the *Arachnida* and *Crustacea*, we shall see that it presents a most remarkable agreement with that of the Insect.

To illustrate this important truth, I might cite Rathke's account of the development of *Astacus* as a type of crustacean embryogeny; but I prefer to speak from my own knowledge, and I will therefore describe the development of *Mysis*, the Opossum-shrimp.

The fertilized ova of this crustacean have a diameter of $\frac{1}{25}$th to $\frac{1}{30}$th of an inch, and consist of a yelk enclosed within a colourless and thin, but strong vitelline membrane.

The yelk is composed of two elements—small and large yelk-masses, the former having about $\frac{1}{3000}$th to $\frac{1}{4000}$th of an inch average diameter, and being usually so closely wedged together as to appear polygonal. The latter are large ($\frac{1}{1000}$th of an inch or more), spherical, and imbedded in the mass formed by the smaller kind of yelk-granules.

I was unable to detect any trace of endoplasts or cells in these ova. Acetic acid developes neither granules nor endoplasts in the yelk-masses. Upon the yelk thus constituted, the blastoderm makes its appearance as a rounded patch, which reflects the light more than the yelk, and therefore appears white by reflected, and dark by transmitted light. The contrast is greatly heightened by the addition of alcohol,[2] or of acetic acid. When the latter reagent has been employed, or even before, if the examination be very carefully conducted, the structure of the blastoderm is seen to be widely different from that of the rest of the yelk. No yelk-granules are visible in it, but it appears to be very finely granular; and embedded within it are

[1] I have no doubt that the *Myriapoda* will be found to exemplify the same morphological laws, with the exception of that relating to the total number of somites in the body, as their congeners; but I find so much that is unsatisfactory in the existing accounts of their development, and so many points in their anatomy requiring re-investigation, that I prefer for the present to be silent about them.

[2] Rathke, in his numerous embryological researches, appears to have constantly availed himself of this property of alcohol in order to render the blastoderm more distinct.

numerous close-set vesicular endoplasts, having a diameter of $\frac{1}{1800}$th to $\frac{1}{2000}$th of an inch. These usually contained many granules, sometimes only one; but I cannot say I have been able to detect any definite nucleolus in them.

The discoid blastoderm is thickest in its middle region, thinning off gradually on both sides, and internally is sharply defined from the substance of the vitellus In the centre it exhibits a more or less marked depression. As development goes on, this depression becomes more and more marked, while the disk thickens and increases circumferentially. At the same time, the layer of yelk in immediate contact with the disk, and co-extensive with it, is found to have a somewhat different constitution from the rest. The globules are large, dark, and sharply defined, and acetic acid gives them a granular appearance, but developes no endoplast.

The depression above alluded to now increases, so as to form a fissure which separates a small tongue-shaped process from the rest of the blastoderm, to which it nevertheless remains closely applied. This process is the rudiment of the abdomen, and in a front view it is rendered more distinct by several clear lines, which mark the commencement of the future caudal bristles. In front of the end of the abdominal process, two minute conical prominences, at first marked by similar, but fewer clear striæ, gradually raise themselves up on each side from the surface of the blastoderm and elongate, their apices being directed backwards. They are the rudiments of the antennules and antennæ.

A delicate structureless membrane is now visible, covering these parts and the adjoining portions of the germinal membrane. It is produced into the terminal setæ of the end of the abdomen and of the two pairs of appendages, and is the commencement of the first skin of the larva.[1]

The anterior part of the blastoderm is wider than the posterior, and is produced into two great lobes divided by a median fissure. These are the "procephalic lobes," and have the same relation to the anterior division of the head as the corresponding parts in the embryo *Aphis*.

In this state the embryo becomes a larva, for it bursts its vitelline envelope and lies naked in the pouch of the mother. The rudimentary abdomen is at the same time extended, so that the little creature is now about $\frac{1}{20}$th of an inch in length, and is very like a pear in shape, the stalk being represented by the abdomen, which is terminated by a flattened, bifid, spinulose fin.

[1] See, for illustrative figures of the development of *Mysis*, my 'Lectures' above cited.

The whole larva is covered by a continuation of the delicate membrane already noticed on the limbs and abdomen. The blastoderm invests the abdomen almost completely, but in front it covers only a somewhat fiddle-shaped area on one face of the yelk. It is still more deeply bilobed in front, and the antennules and antennæ are much elongated. The larva next begins to grow, being doubtless nourished by the fluid contained in the maternal pouch ; and at the same time its ventral region assumes a curve, contrary to that which it originally possessed, becoming more and more convex.

The cephalic region is now clearly distinguishable ; it occupies nearly one-half of the whole length of the body. The procephalic lobes extend upwards over the anterior face of the vitellus, and upon each a large rounded elevation, the rudiment of the ophthalmic peduncle, has made its appearance in front of the antennule. The latter, like the antennæ, elongate greatly, and become divided longitudinally, within the sheath afforded by the primitive integument, into their two terminal branches.

A slight constriction indicates the boundary between the antennulary and antennary sterna, and behind these, similar depressions mark off the surface of the blastoderm into seventeen additional segments.

Attached to them are as many pairs of appendages, which in the youngest larvæ examined had the following form :—

The first pair were rounded massive elevations, situated one on each side of the pit indicating the position of the oral aperture ; from their anterior edge a short oval palp already projects. These are the rudimentary mandibles.

The next pair, or first maxillæ, are small rounded elevations meeting in the middle line. The second maxillæ succeed, and are more elongated, three-jointed, and bent back parallel with one another. The maxillipedes and the thoracic ambulatory legs form one continuous series of similar appendages, all elongated and bent back against the sternal surface of the body.

The abdomen is very short, but is clearly distinguishable from the thorax by its less complete segmentation, and by the rudimentary condition of all its appendages save the last pair.

The blastoderm as yet extends only for a little way on the sides of the body. The primitive larval integument still invests the whole body loosely, but passes smoothly over all the appendages, except the antennules and antennæ, which continue to be ensheathed by it.

The larva remains in this general condition until it attains $\frac{1}{14}$th of an inch in length, the principal differences in its later stages being the

increased growth of the body as compared with the head, the completion of the dorsal surface by the upward extension of the blastoderm, and the gradual restriction of the yelk to the anterior part of the body.

I have been unable to determine, as precisely as in *Aphis*, the exact share taken by the procephalic lobes in the composition of the roof of the head in the crustacean ; but they assuredly extend over a considerable part of its latero-dorsal parietes.

The carapace appears at first as a ridge-like process developed from the dorso-lateral region of the antepenultimate and preceding thoracic and cephalic somites, as far forwards as the bases of the antennules. It is certainly not an extension backwards of the terga of any of the anterior cephalic somites, but is from the first continuous with, and developed from, the thoracic somites.

It is needless to trace the history of the larval *Mysis* further,—what has been said sufficiently proving the close resemblance of its development to that of *Aphis*.

§ 3. *Embryogeny of* Scorpio *as exemplifying* Arachnida.

I have not yet had the opportunity of working out the development of an Arachnidan ; but the researches of Rathke[1] and Herold[2] are so full and clear, that the omission is of little moment.

Rathke's observations on the development of the Scorpion show that after, or even before, the blastoderm has extended over the whole yelk, a papillary elevation appears at one pole. It is the rudiment of the future abdomen, including under that term all the segments of the body behind that which carries the last pair of respiratory organs. In front of this, eleven pairs of closely approximated thickenings make their appearance ; and then, at the sides of the sixth to the tenth pair of them, inclusively, counting from the rudimentary abdomen, papillary processes are developed. It is clear, from Rathke's figures, that the anterior pair of thickenings are the "procephalic lobes," while the succeeding ones are the sterna of the somites between the mouth and the abdomen. The five pairs of processes thrown out by the five anterior of these are the great chelæ and the four pairs of ambulatory appendages. The antennæ make their appearance subsequently from the procephalic lobes (or their junction with the rest of the blastoderm) in front of the mouth. It is not expressly stated, but I do not doubt, from Rathke's figures, that the

[1] Reisebemerkungen aus Taurien, 1837. [2] De Generatione Aranearum, 1824.

upper region of the head is formed, as in *Insecta* and *Crustacea*, by the union of these lobes.

Rathke's account of the number of rudimentary post-oral sterna would lead one to suppose that in the embryo one sternum is wanting. I believe, however, that the truth is, that the sterna of the genital and pectiniferous somites were already so much smaller than the rest in the embryos which Rathke chanced to examine, as to be regarded by him as one.

I base this conclusion upon the condition of the nervous system, which consisted of eleven pairs of clearly distinguishable post-oral cephalo-thoracic ganglia; that is, of just the same number as in an embryonic *Astacus*. Of these, the four posterior were widely separated, and lay in the pulmoniferous somites; while the seven anterior pairs extended only a little way beyond the ambulatory appendages, and were united into a triangular mass. The anterior of these ganglia were the largest, the posterior the smallest. The anterior pair gave off the nerves to the chelæ.

It would be difficult to obtain a more clear and conclusive proof than this, that the chelæ of the Scorpion are the homologues of the mandibles of the Crustacean, and that the succeeding somites, as far as the last pulmoniferous one, correspond with the fifth to the fourteenth somites, inclusively, of the typical Crustacean. The six succeeding somites are the homologues of the six abdominal somites of the Crustacean; the aculeated sting corresponds with the telson; and the only difference presented by the pre-oral somites is that common to all air-breathing *Articulata*, viz. the sessile eyes, and the non-development of one of the pairs of antennæ.

§ 4. *Generalizations regarding the Embryogeny of the* Articulata, *and Morphological Laws based on these.*

From all these facts of development, I deduce the following morphological laws (some of which have already been enunciated for particular classes) for the *Articulata* (*Insecta*, *Arachnida*, *Crustacea*) generally.

1. The first-formed rudiment of the embryo corresponds with its sternal surface, or with the side upon which the great centres of the nervous system are placed. It is a neural rudiment.

2. In the thorax and abdomen this neural rudiment grows up on each side towards the tergal region, or that on which the great centre of the circulation is placed.

3. In the Articulate embryo, therefore, the neural wall is formed first, and gradually extends tergally so as to form the hæmal wall.

4. The cephalic blastoderm very early undergoes a peculiar flexure, a greater or less portion in front of the mandibles being bent up at right angles to the rest, and even in many instances extending backwards, so as to constitute the entire hæmal region of the head. In these cases the top of the head is in reality a sternal, and not a tergal surface.

As a consequence of this flexure, the line of attachment of the bases of the eyes and antennæ is frequently altogether above that of the other appendages, so that they appear to be tergal, and not sternal, appendages.

5. The anterior extremity of the cephalic blastoderm becomes early divided by a median fissure, each lateral portion being a "procephalic lobe." In Insects the line of junction of these procephalic lobes is the epicranial suture.

6. In *Insecta* and *Crustacea* the head, in the embryo, is easily distinguishable from the rest of the body. In Podophthalmous *Crustacea* it is clearly seen to be composed of six somites, each possessing a pair of appendages; of these, the first are the eyes; the second, the antennules; the third, the antennæ; the fourth, the mandibles; the fifth, the first maxillæ; and the sixth, the second maxillæ.

In *Insecta*, on the other hand, only four pairs of appendages appear in the head, the eyes being sessile, and one pair of antennary organs remaining undeveloped.

In the *Arachnida* it appears to me to be quite clearly shown by development that the anterior pair of appendages are antennæ; the second pair, mandibles, with a hugely developed palpus; the third pair, first maxillæ; and the fourth pair, second maxillæ, converted, like the next two pairs of appendages, into ambulatory legs.

It follows, therefore, if we take the number of moveable appendages as the test, that in the *Articulata* never more than six, and never fewer than four, somites enter into the composition of the head. But is the number of moveable appendages a just test of the number of somites entering into a part? No one will pretend that it is so in the abdominal and thoracic regions; and if we consider the head of *Crustacea* alone, we find the eyes becoming sessile, and one pair of antennary organs aborting, without the least reason for concluding that the typical structure of the head is altered. It seems to me, then, hardly a hypothesis to assume that the sessile eyes of Insects represent the appendages of a somite, since it is universally

admitted that they do so in *Edriophthalmia*. But by this assumption we arrive at a still closer approximation of the different classes in regard to their cephalic structure; for all would, on this supposition, have either five or six cephalic somites,—the former number being invariably met with in the true air-breathers (though in many purely aquatic forms also), while the latter is found only in those which respire by means of gills.

I repeat, I can see nothing in this generalization but a simple expression of the facts. But I would go a step further, and add to this the *hypothesis*, that in the *Articulata* the head is normally composed of six somites, which are all fully developed only in *Podophthalmia*, *Stomapoda*, and some *Branchiopoda*; while in other *Crustacea*, some one or more of the pre-oral somites is more or less abortive, and in *Arachnida* and *Insecta*, the appendages of the first somite are sessile, and those of the second or third undeveloped. Admitting this hypothesis, I find further, that of the six cephalic somites, the sterna of three (the mandibular and two maxillary) are always situated behind the mouth and on the ventral surface of the body. The position of the other three varies; but the most anterior or ophthalmic is always bent upwards in consequence of the cephalic flexure, and not unfrequently, as in Insects, constitutes the greater part, or the whole, of the dorsal region of the head. The next two, or antennulary and antennary sterna, may present every variation from approximative parallelism with the axis, in *Squilla*, to extreme reflexion, as in *Insecta* and many *Crustacea*.

7. Nothing can be more variable than the number of the somites whence appendages are developed in the various classes and orders of the *Articulata*; and in the *Myriapoda* the total number of somites even is susceptible of an extreme amount of variation. But in the other classes it appears to me that there is a typical number of somites, from whence but comparatively few forms depart either by way of excess or defect. Thus, if we leave out the *Læmodipoda*, all Podophthalmous and Edriophthalmous *Crustacea* have twenty somites, of which six are cephalic, eight thoracic, and six abdominal. In a very few *Branchiopoda*, and in *Trilobita*, there is more than the typical number of somites; but I believe that in all other *Crustacea*, where the number of somites is not twenty, it is less.

The question of the typical number of somites in the body of the *Insecta* is one which has been much discussed. But all the theories on this subject with which I am acquainted are, in my apprehension, vitiated by the mistaken view which their authors take of the composition of the Insect's head. Many seem to consider it to be a

simple segment; while those who admit a multiplicity of segments, appear to be misled by the position of the eyes and antennæ, into regarding them as tergal appendages of the segments over whose sternal appendages they lie—as a kind of wings of the cephalic somites, in short. Again, it is supposed by many that the labrum and the lingua are the representatives of the appendages of distinct somites, a conception which is at once negatived by the study of their development.

As I have endeavoured to show, there are certainly five, and hypothetically six, somites in the head of *Insecta*; there are certainly at least three in the thorax; but the number in the abdomen has been as much disputed as the number in the head. Zaddach considers, as a general rule, ten to be the number of abdominal somites in Insect larvæ; Westwood and Newport enumerate eleven in some *Hymenoptera*, and this last is, I believe, the maximum number of somites which has yet been found in the abdomen. Now, if we assume the number of somites in the head to be six, the number in the thorax three, and the number in the abdomen eleven, we shall arrive at twenty as the maximum number of somites in the body of an Insect.

This conclusion is in remarkably close accordance with the results obtained by M. Lacaze-Duthiers from his laborious and remarkable researches into the structure of the female genital apparatus of *Insecta*. M. Duthiers finds that the vulva always opens between the eighth and ninth abdominal somites, and that in *Neuroptera*, in *Orthoptera*, in most *Hemiptera*, and in *Thysanura*, three somites intervene between the vulva and the anus, which is always placed at the very extremity of the body. There are thus eleven abdominal somites, and, therefore, a total number of twenty, in these four orders.

Some *Hemiptera* have the last abdominal somite abortive, and this appears to me to be the case in *Aphis*. In *Coleoptera* and *Hymenoptera*, the tenth and eleventh somites abort, nine only remaining: in *Lepidoptera*, finally, all three post-genital somites remain undeveloped. M. Lacaze-Duthiers' researches tend to show that a fundamental unity prevails amidst those apparently most diverse apparatuses which we know as stings, borers, and ovipositors, and that they are always the result of a modification undergone by the ninth abdominal somite.

I do not consider myself competent to give an opinion as to the details of the investigations to which I have just alluded, but I cannot refrain from expressing the belief that the labours of

future investigators will bring only a confirmation of their general accuracy.

The only adult Insect, besides *Aphis*, which I have studied with sufficient care in reference to these views, is the common Cockroach (*Blatta orientalis*), an insect which I can recommend as admirably adapted for investigation. Here it is very easy to find the eleven abdominal somites, and to satisfy oneself that the vulva is placed between the eighth and ninth, and that the two outer elongated pieces of the curious clasping apparatus for the ovisacs are formed by a modification of parts of the ninth somite. The smaller and inner processes, on the other hand, are clearly developed from the sternum of the tenth somite, while the lateral anal valves represent the eleventh somite.

I have found that while the vulva opens between the eighth and ninth somites, the aperture of the spermatheca is situated on the sternum of the ninth, and that of the colleterial glands on the sternum of the tenth somite.

In the male the complex penis is formed by a modification of the tenth somite, and the aperture of the vas deferens is on the sternum of this somite, or between it and the eleventh.

Weighing all these facts, the conclusion to which they point seems obvious, viz. that in *Insecta*, as in *Crustacea*, the typical number of the somites is twenty.

I have shown above that the development of the Scorpion proves that there are seventeen post-oral somites besides the sting (which is plainly the homologue of the telson in the *Crustacea*) in this Arachnidan. If we make the same assumption for the Scorpion as for the Insect, that one of the antennary somites is abortive, we shall have a total of twenty somites here also. The anatomy of the adult Scorpion appears to me fully to confirm this view. Beginning at the hinder end, we find, including the telson, six segments behind those which carry the respiratory apertures. Of these there are four; and in the three posterior, the sternum has nearly the same length as the tergum; but in the anterior one the sternum is much longer than the tergum. Furthermore, these sterna at first seem to occupy the whole space up to the posterior boundary of the cephalothorax, while, on the dorsal side, two narrow terga lie between the tergum corresponding with the anterior sternum and the cephalothorax.

It appears, therefore, as if there were two more terga than sterna in the abdomen; but on more careful investigation, the missing sterna show themselves as the supports of the pectines and of the genital aperture in front of these last curious organs. Indications of the

terga which belong to the two posterior pairs of ambulatory limbs are clearly visible on the posterior part of the cephalothorax, and these limbs are strongly distinguished from the anterior two pairs by the absence of the triangular processes directed towards the mouth, which characterize the bases of the latter. Indeed, the anterior ambulatory legs, by means of these processes, take part in the formation of the oral cavity as completely as do the maxillæ of any other Articulate animal.

Another exceedingly natural demarcation between the two anterior and two posterior pairs of ambulatory limbs is afforded by the so-called 'diaphragm' which divides the thoracic from the cephalic cavity, and whose attachment corresponds with the interval between these two sets of appendages.

In *Galeodes*, the two posterior pairs of ambulatory legs are attached to distinct segments.

There is no necessity to enter into any disquisition upon the homology of the appendages and the general uniformity in plan, so far as the anterior part of the body is concerned, in all *Arachnida*. But it may be asked, what becomes of the hinder thoracic and the abdominal somites in the Spiders and Mites? Without, at present, giving a positive answer to this question, I am inclined to think that the Spiders stand to the Scorpion in the relation of *Læmodipoda* to *Amphipoda*, and that many of their posterior somites are aborted.

I do not doubt that many minor variations will be detected when the morphology of the *Articulata* is carefully examined; but I venture to think it a result of no small moment, if it can be proved that a Lobster, a Cockroach, and a Scorpion are composed of the same primitive number of somites; that the head in each consists of the same number of parts, and that the great differences are the consequence of the different modification of the thoracico-abdominal somites, all fourteen of which bear appendages in the Lobster, while only three (or if we consider the genital apparatus in the light of appendages, five) are so provided in the Insect, and only two (leaving out of consideration the "pectines") in the Scorpion.

8. I have elsewhere[1] explained at length my views with regard to the nature of the carapace in the *Crustacea*, and I will only repeat here, that there seems to me to be no constancy in its composition. The rudimentary carapace of *Squilla* is assuredly developed from not more than four somites, the antennary, mandibular, and maxillary. In *Apus*, I doubt whether more than the six cephalic somites enter into its composition. In *Cuma* it is constituted by the cephalic and

[1] 'Lectures,' Med. Times and Gazette, 1857.

three anterior thoracic somites, in *Mysis* by the cephalic and six or seven anterior thoracic, and in ordinary *Podophthalmia* by all the cephalic and thoracic somites.

9. Lastly, there are certain parts developed singly in the median line in the *Articulata*. Of this nature are the frontal spines of *Crustacea*, their telson, and the sting of the Scorpion, whose mode of development appears to be precisely similar to that of a telson. In the same category we must rank the labrum in front of the mouth, which in the *Crustacea* (at least) appears to be developed from the sternum of the antennary or third somite, the metastoma (or so-called labium or lingua) of *Crustacea*, and the lingua of *Insecta*, behind the oral aperture.

However much these appendages may occasionally simulate, or play the part of, appendages, it is important to remember that, morphologically, they are of a very different nature, and that the confusing them with true appendages must tend completely to obscure the beautiful relations which obtain among the different classes of the *Articulata*.

§ 5. *The Embryogeny of the* Articulata, Mollusca, *and* Vertebrata *compared.*

I find it difficult to conclude this memoir without saying a few words on the resemblances and differences between the embryogenic changes of the *Articulata* and those of the *Mollusca* and *Vertebrata*. Absolute and fundamental differences appear to me to separate the members of these three classes almost from the first appearance o the germ.

As we have seen, it is the neural side of the Arthropod which is first developed, while, so far as I am aware, it is the opposite or hæmal side which is first formed in every Mollusk. The germ of the Arthropod becomes antero-posteriorly segmented; the germ of the Mollusk never does so. From these two fundamental differences a multitude of others necessarily follow.

The Articulate embryo is no less markedly separated from that of a Vertebrate animal, although in the latter, as in the former, it is the neural surface which is first developed; for I know of nothing in the Articulate embryo to be compared with the primitive groove, the chorda dorsalis, and the dorsal plates of the Vertebrate.[1] They, like

[1] I therefore by no means agree with what Zaddach says on this subject, or with regard to the homologue of the amnion in *Articulata*.

the amnion and the allantois, are, I believe, structures without a representative in the other two sub-kingdoms.

There is perhaps, as Zaddach maintains, a certain analogy between the primitive segments of the Articulate animal and the primitive vertebræ ("Urwirbel" of Remak) in the Vertebrate, but with the commencing differentiation into tissues the resemblance entirely ceases. The appendages of the Vertebrate embryo are more Molluscan than Articulate in their primitive mode of development. Notwithstanding all these great and real differences, however, there appears to me to be one respect in which a most singular analogy obtains between the Vertebrate and the Articulate type :—it is in the construction of the head.

Adopting, in some respects, the views of Professor Goodsir,[1] I can recognize at least six more or less complete segments in the completely ossified Vertebrate cranium. It is clear that the Vertebrate mouth opens like that of the Articulate animal, though on the opposite side of the body, between an anterior and a posterior set of cephalic segments. In the interior of the cranium a no less natural boundary between the anterior and the posterior set of cephalic segments is afforded by the pituitary body and its fossa, when the latter exists.

I find, again, in the cranio-facial bend of the base of the cranium in the Vertebrate embryo, something wonderfully similar to the cephalic flexure of the Articulate head, and in the cranial trabeculæ (Schädel-balken of Rathke), analogues of the procephalic lobes.

While fully recognizing the fundamental differences between the Articulate and the Vertebrate type, then, I think we should greatly err if we overlooked such singular analogies as these. Future research will show whether they are or are not the outward signs of a deeper internal harmony than has yet been discerned, between the *Articulata* and *Vertebrata*.

Since the present memoir was read to the Society, some additional facts of importance have come to my knowledge. In the first place, my friend Mr. Lubbock, having undertaken to work out the development of *Coccus*, was led thereby to search for what I have called "ovarian glands" in other insects. His results will be published at length elsewhere; but he permits me to say that corresponding organs exist in all *Lepidoptera*, *Hymenoptera*, Geodephagous and Hydrodephagous *Coleoptera*, *Diptera*, and most *Neuroptera*, while they are absent in *Orthoptera*, *Pulex*, *Libellulidæ*, &c., and are all terminal, instead of forming groups between the egg-germs, in the non-

[1] As expressed in the Edinburgh New Philosophical Journal, 1857, p. 118 *et seq.*

geodephagous *Coleoptera* and *Hemiptera*. They have been figured in *Lepidoptera* by Herold, Meckel, Thompson, and Stein, in *Diptera* by Stein and Leuckart, and in *Coleoptera* by Stein.

Secondly. In September last I received the fourth Part of the fourth volume of Moleschott's 'Untersuchungen,' which contains a long and remarkable Essay by Leuckart, "Zur Kenntniss des Generations-wechsels und der Parthenogenesis bei den Insekten." The first article in the memoir is on the "Alternation of Generations in the *Aphides*." The author describes at length, and figures, the female reproductive organs of *Aphis Padi*; and although the arrangement of these organs is somewhat different from what obtains in my *Vacuna*, I am happy to say that his account of the ultimate structure of the ovaries essentially coincides with mine. The view which Leuckart takes of the relation of the ova and agamic germs (p. 346) is also in close agreement with my own. I lay the more weight upon these coincidences because Professor Leuckart's observations must have been made at the same time with, and were of course wholly independent of, mine.

Lastly, not having the works of either Kaltenbach or Koch at hand when my memoir was read, I abstained from attempting to give the specific names of my *Aphides*. I have no doubt now that the viviparous form is the *Aphis Pelargonii* of Kaltenbach, especially as my friend Mr. Dallas, who has paid particular attention to the *Hemiptera*, is of that opinion. The oviparous female resembles so much in form and habit the *Vacuna dryophila* of Schrank, that I have little doubt it is really that species, though, when carefully examined, the antennæ are found to have six unquestionable joints, and seven, if the swollen base of the last division of the antennæ is to be regarded, as I believe it should be, as a distinct joint. The eyes also have a small and inconspicuous tubercle; and the promuscis is not nearly so long as either Kaltenbach or Koch states.—*Nov.* 16, 1858.

[PLATE 1]

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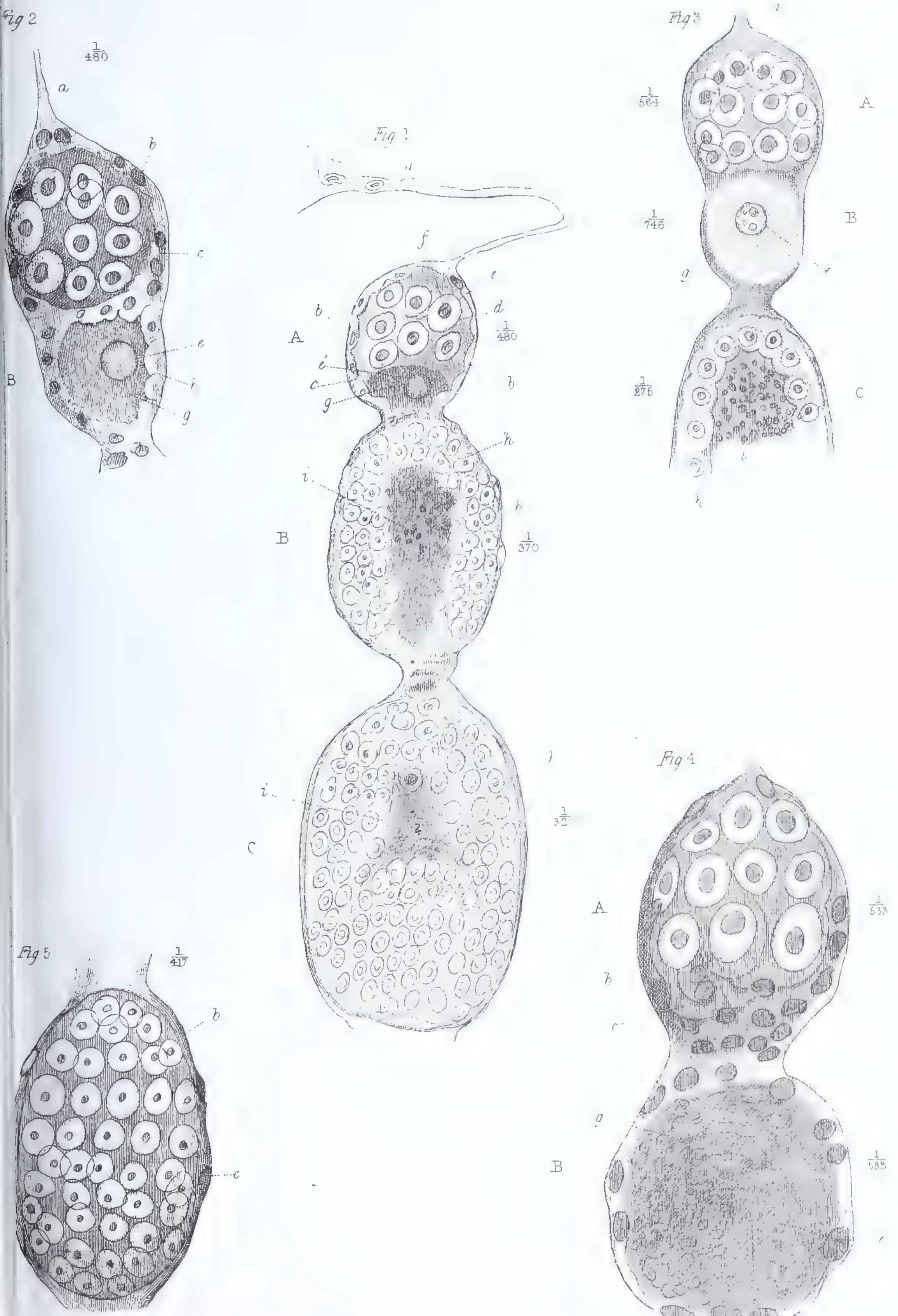

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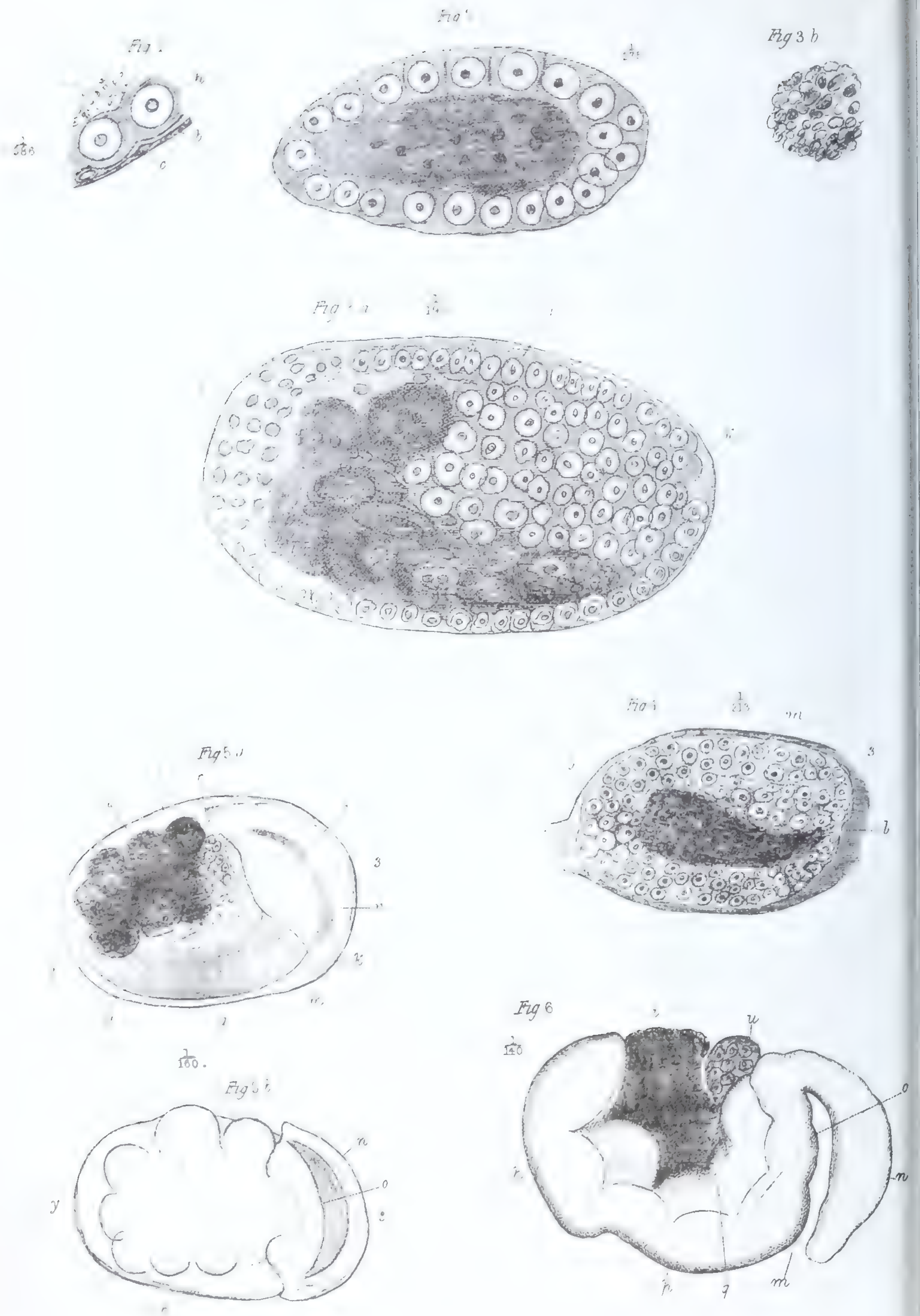
[PLATE 8]



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DESCRIPTION OF THE PLATES.

TAB. XXXVI. [PLATE 1].

Aphis Pelargonii.

The letters have the same signification throughout. The fractions indicate the measured size, in parts of an inch, of the objects.

Fig. 1. The three anterior chambers of a pseudovarium: A. the apical chamber; B. the second; C. the third. *a.* Pseudovarian ligament; *b.* wall of the pseudovarium; *c.* its epithelium; *d.* periplast or homogeneous matrix of the apical chamber; *e.* clear vesicle; *f.* its endoplast, the two corresponding with the germinal vesicle and spot of an ovum; *g.* a pseudovum partially detached, its periplast greatly enlarged; *e'.* its vesicle, whose endoplast is invisible; *h.* blastoderm; *i.* pseudovitellus.

Fig. 2. Terminal chamber of a pseudovarium, with the second chamber beginning to be formed in consequence of the enlargement of the pseudovum (*g*), which is about $\frac{1}{960}$th of an inch in diameter.

Fig. 3. The pseudovum is still more enlarged, and the second chamber is nearly distinct. The vesicle, *e'*, remains, and exhibits certain indistinct granules in its contents. The cells of the blastoderm of C measure about $\frac{1}{2500}$th of an inch in diameter.

Fig. 4. The second chamber is quite distinct from the first, and contains a mass (*g*) in which no clear vesicle could be discovered: this mass became clearer and irregularly areolate by the action of water.

Fig. 5. The cellular germ-mass. The cells or clear cavities have a diameter of about $\frac{1}{3200}$th of an inch; their endoplasts are hardly more than $\frac{1}{10000}$th of an inch in diameter.

TAB. XXXVII. [PLATE 2].

Aphis Pelargonii. Letters as before.

Fig. 1. A portion of the blastoderm and pseudovitellus of an unaltered germ, only $\frac{1}{386}$th of an inch in length, but otherwise like the preceding. The clear vesicles measured $\frac{1}{3200}$th of an inch; the endoplasts $\frac{1}{18000}$th.

Fig. 2. A germ extracted from its chamber and treated with acetic acid. It has no pseudovitelline membrane.

Fig. 3 *a.* A germ extracted from its chamber. It is enclosed within a pseudovitelline membrane (*k*); and its pseudovitellus is arranged in obscure spheroids, of which one is represented in 3 *b.* acted on by water. Its granules are about $\frac{1}{9000}$th of an inch in diameter.

Fig. 4. Germ $\frac{1}{215}$th of an inch in length. The cells of the posterior end (3) present a sort of break (*l*), and the blastoderm on one side is greatly thickened. The thickened portion offers an indication of a division (*m*). The anterior end (*y*) is also somewhat thickened.

Fig. 5 *a.* Germ $\frac{1}{160}$th of an inch, enclosed within its pseudovitelline membrane: *n.* rudiment of the abdomen; *o.* of the thorax; *p.* of the head; *l'.* gap corresponding with *l*, and now filled by the pseudovitellus; *q.* inner layer of the germ; *r.* that portion of it which will become the pseudovarium. 5 *b.* Diagrammatic view of the same, viewed from above.

Fig. 6. Lateral view of a larger germ without its pseudovitelline membrane. The anterior part of the cephalic blastoderm (*p*) has extended upwards, and constitutes the procephalic lobe *p'*. The rudiment of the pseudovarium (*r*) is still more distinct than in the preceding.

TAB. XXXVIII. [PLATE 3].

Aphis Pelargonii.

Fig. I. Embryo enclosed within its pseudovitelline membrane. The pseudovitellus has aggregated over the abdomen, and more or less completely left the thorax. Letters as before except—*s.* the first larval integument; *lb.* labrum; *at.* antenna; IV′. mandible; V′. first maxilla; VI′. second maxilla; VII′. first, VIII′. second, and IX′. third thoracic leg. I *a.* The same embryo seen from below.

Fig. 2. Embryo of the same size, viewed from below and the side, the blastoderm unfolded, and the appendages separated.

Fig. 3. Highly magnified view of part of the pseudovitellus, and of the rudiment of the pseudovarium, in an embryo $\frac{1}{90}$th of an inch in length.

Fig. 4. Embryo $\frac{1}{84}$th of an inch, enclosed in its pseudovitelline membrane.

Fig. 5. Embryo $\frac{1}{70}$th of an inch, in its pseudovarian chamber.

TAB. XXXIX. [PLATE 4].

Aphis Pelargonii.

Fig. I. A. Nearly full-grown fœtus, extracted from its investments, and somewhat unfolded: *t.* anus, whence the alimentary canal is seen taking a curved S-like course to the mouth. B. Terminal chamber of one of the pseudovarial cæca of this embryo.

Fig. 2. The mouth of this embryo seen from below. The "labium" (VI′) already appears as a large single process bilobed at its free end.

Fig. 3. Side view of the head of a similar embryo, showing the relative position of the different appendages and the course of the œsophagus.

Fig. 4. A nearly full-grown fœtus in its pseudovitelline membrane: I′. the pigment of the eye; *s.* rudimentary siphons.

Fig. 5. A partially diagrammatic figure of the wingless viviparous form of *Aphis Pelargonii.* The Roman numbers indicate the typical somites of the body and their appendages; the other numbers mark the abdominal somites. A. Anus; G. genital aperture; S. siphon.

TAB. XL. [PLATE 5].

Reproductive Organs of the oviparous Aphis (Vacuna dryophila).

Fig. I. The female organs entire. One ovarian cæcum only is represented; and I have purposely selected one of those, the ovarian glands in whose apical chamber are very similar, at first sight, to ova. A. Anus; B. vulva; C. vagina; D. oviducts; E, F, G, H, I, K. chambers of the ovary; L. ovarian glands; *m.* colleterial glands; *n.* spermatheca; 7, 8. seventh and eighth abdominal sterna.

Fig. 2. The three anterior chambers of an average ovarian cæcum. Letters as before, with the addition of—*o.* germinal vesicle of the nascent ova in the terminal chamber (K); *o′.* germinal vesicle of ovum in I; and *o″.* of ovum in H; *p.* epithelium; *q.* cord-like secretion of ovarian gland (*l*); *l′.* inner capsule of ovarian gland.

Fig. 3. The end of another ovarian cæcum, showing very distinctly the apparent continuity of the cord, *q*, with the ovum in the third chamber. The granules of the viscid vitelline mass (which is surrounded by no membrane) are so numerous as to hide the germinal vesicle.

Fig. 4. A. Posterior extremity of the ovum unaltered: *r.* chorion; *s.* tubercular elevation; *t.* appendage; *u.* its gelatinous investment; *v.* rod-like bodies embedded therein; *v′.* the same more magnified. B. Anterior end of the ovum after the action of potash; *y.* papillary elevation; *z.* internal markings of the chorion (*r*); *w.* vitelline membrane; *x.* vitellus. C. Posterior extremity treated in the same way: *s′.* micropyle?

[PLATE 3]

Fig 1

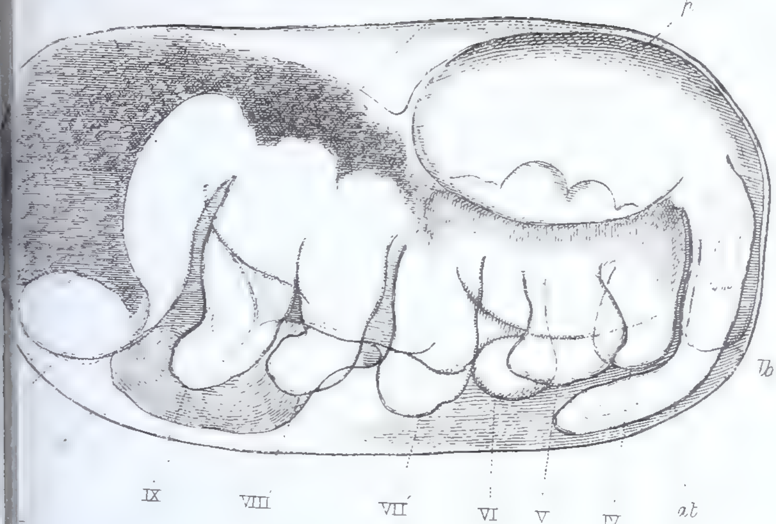
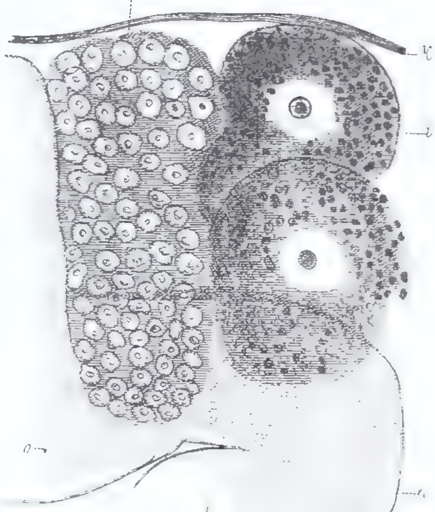


Fig 3



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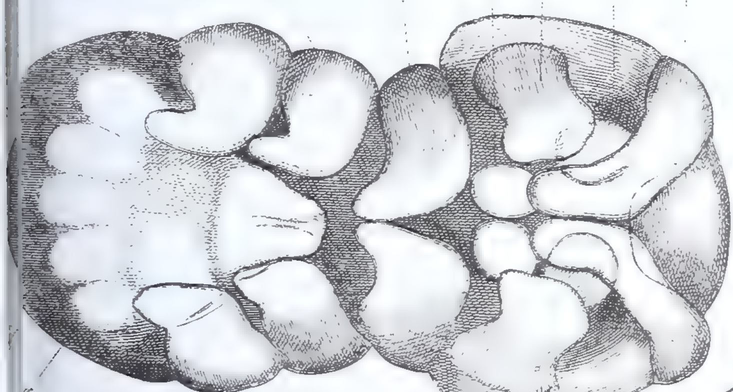

Fig. 1a

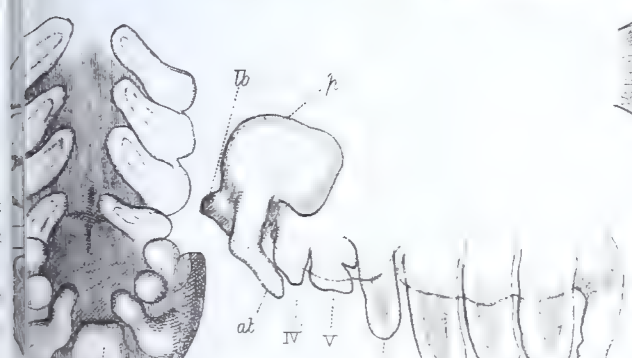

Fig. 2

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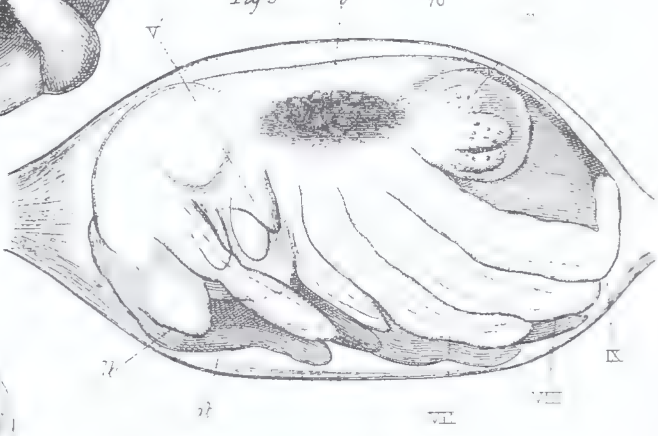
Fig 5 1/70



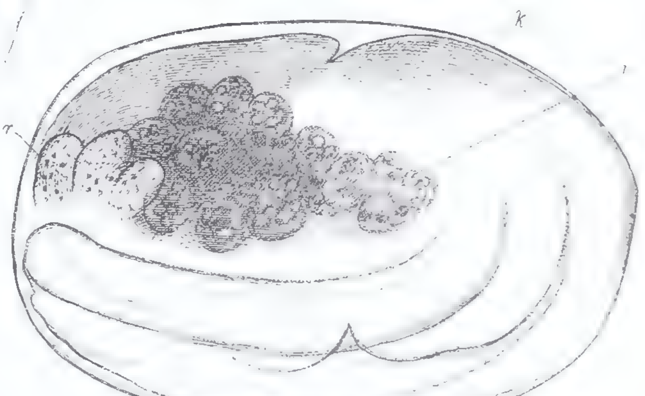


Fig 4

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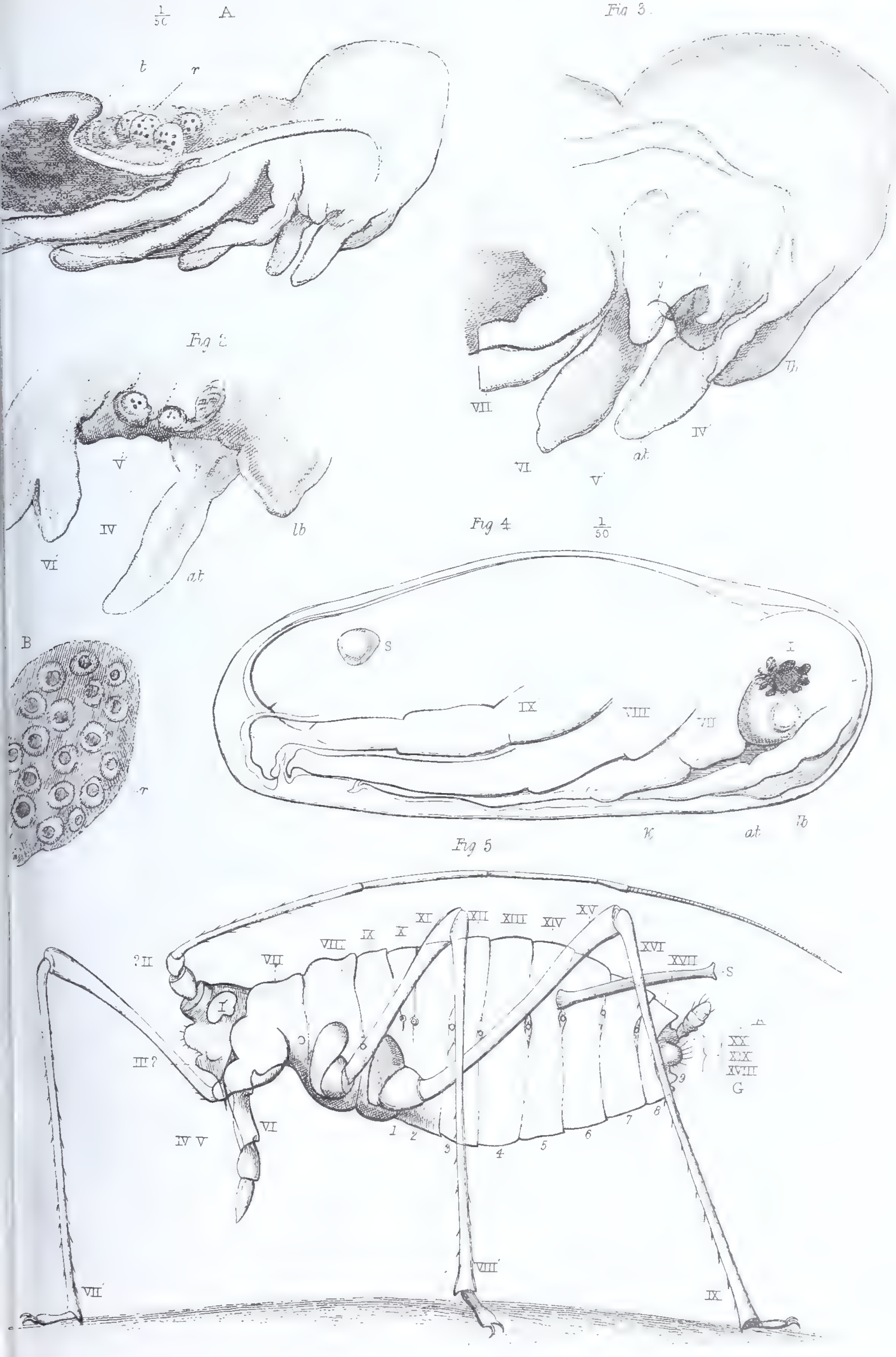
[PLATE 4]



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III

ON SOME POINTS IN THE ANATOMY OF NAUTILUS POMPILIUS

Journal of the Linnean Society, vol. iii. 1859 (*Zool.*), *pp.* 36–44. (*Read June 3rd*, 1858.)

SOME time ago my friend Dr. Sinclair, of New Zealand, had the kindness to offer me two specimens of the Pearly Nautilus which had been brought to him from New Caledonia, preserved in Goadby's solution. I gladly accepted the present, and looked forward to the dissection of the rare animal with no little pleasure; but on proceeding to examine one of the specimens, I found its anatomical value greatly diminished by the manner in which a deposit from the solution had glued together some of the internal viscera. Other parts of the Nautilus, however, were in a very good state of preservation; and I have noted down such novel and interesting peculiarities as they presented, in the hope that an account of them will be acceptable to the Linnean Society.

Of the six apertures which, besides the genital and anal outlets, open into the branchial cavity of *Nautilus pompilius*, one on each side lies immediately above and in front of that fold of the inner wall of the mantle which forms the lower root of the smaller and inner gill, and encloses the branchial vein of that gill. The aperture is elongated and narrow, with rather prominent lips. It measures about $\frac{1}{8}$th of an inch.

The other two apertures are larger, and lie at a distance of $\frac{7}{16}$ths of an inch below and behind the other. They are in close juxtaposition, being separated only by a thin triangular fold of membrane, which constitutes the inner lip of the one and the outer lip of the other.

The inner aperture is the larger, measuring $\frac{3}{16}$ths of an inch in long diameter, and having the form of a triangle with its base directed posteriorly. The outer aperture is not more than $\frac{1}{8}$th of an inch long.

The two apertures lie just above the edge of the fold of membrane which runs from the inner root of the larger or outer branchia, across the branchial cavity and beneath the rectum, to the other side.

These apertures lead into five sacs, which collectively constitute what has been described as the pericardium. The sacs into which the superior apertures open, by a short wide canal with folded walls, are situated on each side of and above the rectum. Their inner boundaries are separated by a space of not less than $\frac{5}{8}$ths of an inch in width, in which lie the vena cava and the oviduct. Each cavity has a rounded circumference, and a transverse diameter of about half an inch. In a direction at right angles to this diameter the dimensions vary with its state of distention; but a quarter of an inch would be a fair average.

The anterior or outer wall of the cavity is formed by the mantle; the posterior, inner, or visceral wall by a delicate membrane. The former separates it from the branchial cavity; the latter from the fifth sac, to be described by-and-by. I could find no natural aperture in the thin inner wall, so that I conceive no communication can take place between either of these sacs and the fifth sac.

Two irregular, flattened, brownish, soft plates depend from the posterior wall of the sac into its cavity; their attached edges are fixed along a line which is directed from behind obliquely forwards and upwards.

The outer and smaller of the inferior apertures on each side leads into a sac of similar dimensions and constitution to the preceding, but having a less rounded outline in consequence of its being flattened in one direction against its fellow of the opposite side, from which it is separated only by a delicate membranous wall, whilst on another side it is applied against the inferior wall of the superior sac, and is in like manner separated from it only by a thin and membranous partition.

Like the upper sacs, each of these has two dark-brown, lamellar, glandular masses depending from its membranous visceral wall.

A delicate, but broad, triangular membranous process, about $\frac{1}{4}$th of an inch long, hangs down freely from the visceral wall of the cavity just behind the opening of the short canal which connects the sac with its aperture.

The third and largest aperture on each side opens directly into a very large fifth cavity, whose boundary is formed anteriorly by the visceral walls of the sacs already described, and behind this by the mantle itself as far as the horny band which marks and connects the insertion of the shell-muscles.

In fact this cavity may be said to be co-extensive with the attached part of the mantle,—the viscera, enclosed within their delicate "peritoneal" membranous coat, projecting into and nearly filling it, but nevertheless leaving a clear space between themselves and the delicate posterior wall of the mantle.

A layer of the "peritoneal" membrane extends from the posterior edge of the muscular expansion which lies between the shell-muscles and from the upper wall of the dilatation of the vena cava, and passes upwards and backwards like a diaphragm to the under surfaces of the gizzard and liver. It is traversed by the aorta, to whose coats it closely adheres.

Along a line nearly corresponding with the horny band which proceeds from the insertions of the shell-muscles and encircles the mantle below, the pallial wall is produced inwards and forwards into a membranous fold or ligament, which I will call the pallio-visceral ligament; and this pallio-visceral ligament becoming attached to various viscera, divides the great fifth chamber into an anterior inferior, and a posterior superior portion, which communicate freely with one another.

Commencing with its extreme right-hand end, the ligament is inserted into the line of reflection of the mantle, and then into the wall of the oviduct, which becomes enclosed as it were within the ligament. The latter then ends in a free edge on the inner side of the oviduct, and is continued along it until it reaches the inferior surface of the apex of the ovary, into which it is inserted.

The free edge is arcuated; and the rectum passes over it, but is in no way connected with it.

Here, therefore, is one great passage of communication between the anterior and posterior divisions of the fifth chamber.

On the left side this aperture is limited by the heart, whose posterior edge is, on the left side, connected by means of a ligamentous band with the surface of the apex of the ovary; but on the right, for the greater part of its extent, receives a process of the pallio-visceral ligament. Between the ovario-cardiac ligament and this process lies the small oval aperture already described by Professor Owen, which gives passage to the siphonal artery. It constitutes the middle aperture of communication between the two divisions of the fifth chamber.

The left-hand end of the ligament is inserted into the upper wall of the dilated end of the vena cava; but between this point and the heart it has a free arcuated edge, as on the right side.

Thus there are in reality three apertures of communication between

the two divisions of the fifth chamber, the middle, by far the smallest, being alone hitherto known.

A delicate membranous band passes from the whole length of the middle line of the rectum to the heart and to the ovary.

The singular "pyriform appendage" of the heart lies in the left process of the ligament, its anterior edge nearly following the arcuated contour of that process.

The siphuncular process of the mantle was broken in my specimen; but its aperture appeared to communicate quite freely with the posterior division of the fifth chamber.

Four sets of brownish, glandular-looking bodies depend into the anterior division of the fifth chamber, from parts of the delicate septa dividing this from the four small sacs, corresponding with the insertions of the glandular bodies above described.

In fact, on distending the vena cava with air, it is found that the four branchial arteries traverse these septa, and that the appendages in question are diverticula of their walls. Consequently the anterior wall of each branchial vein is produced into two glandular appendages, which hang into one of the four smaller sacs, while the posterior wall is produced into a single mass of appendages, which hangs into the anterior division of the fifth chamber.

Although, as I believe, the five chambers do not communicate directly, all the appendages must nevertheless be equally bathed with sea-water, which enters by the apertures of the chambers.

An impacted yellowish-white concretionary matter filled the anterior chamber; and a small quantity of it lay as a fine powder at the bottom of the posterior one. In the latter, however, its presence might, by possibility, have been accidental. My colleague, Dr. Percy, who kindly undertook to examine this substance, informs me that he has been unable to detect uric acid in it. The follicular appendages of the branchial arteries present remarkable differences in their external appearance. The eight which hang into the four anterior chambers are similar, slightly festooned, but otherwise simple lamellæ; while the four which depend into the posterior chambers are produced into a number of papillary processes. This external difference is obvious enough: whether it be accompanied by a corresponding discrepancy in minute structure I am unable to say; for I have not as yet been able to arrive at any satisfactory results from the microscopic examination of the altered tissues, and, as will be seen below, the only observer who has had the opportunity of examining the Nautilus in the fresh state has not noted any difference of structure in the two sets of follicles.

One is naturally led to seek among other mollusks for a structure analogous to the vast posterior aquiferous chamber of the Nautilus; and it appears to me that something quite similar is offered by the *Ascidioida* and the *Brachiopoda.* In both cases, the viscera, inclosed within a delicate tissue, project into a large cavity communicating freely with the exterior by the cloacal aperture in the one case, and by the funnel-shaped channels which have been miscalled "hearts" in the other.

The rudimentary renal organs of the Ascidian are developed in the walls of the cavity in question; and an aquiferous chamber of

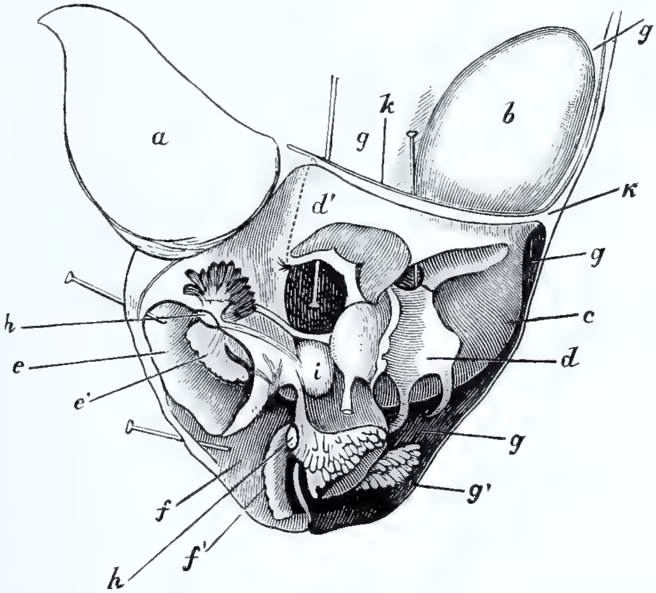


FIG. I.—*Nautilus pompilius.* Viewed from the left side and a little behind. Two of the anterior chambers, and the fifth or posterior chamber, laid open. Natural size.

a. Shell muscle. *b.* Ovary. *c.* Intestine. *d.* Heart. *d'.* Its pyriform appendage. *e.* Superior anterior chamber; *e'.* Its follicles. *f.* Inferior anterior chamber; *f'.* Its follicles. *g.* Posterior chamber; *g'.* Follicles. *h.* Cut ends of branchial arteries. *i.* Termination of vena cava. *k.* Pallio-visceral ligament.

smaller dimensions has the same relation to the kidney in Lamellibranchiata—in Gasteropoda, Heteropoda, Pteropoda, and dibranchiate Cephalopoda. But although such is likely enough to be the case, we do not know at present that the aquiferous chambers in any of the last named mollusks attain an extension similar to that which obtains in Nautilus.

On comparing the observations detailed above with the statements of previous writers, I find that, in his well-known "Memoir on the Pearly Nautilus" (1832), Professor Owen describes "on each side, at the roots of the branchiæ," "a small mamillary eminence with a

transverse slit which conducts from the branchial cavity into the pericardium. There is, moreover, a foramen at the lower part of the cavity (*o*, pl. 5) permitting the escape of a small vessel; and by the side of this vessel a free passage is continued between the gizzard and ovary into the membranous tube or siphon that traverses the divisions of the shell, thus establishing a communication between the interior of that tube and the exterior of the animal."

The foramen here described is easily seen; but, as I have stated, there are other modes of communication between the so-called pericardium and the cavity with which the siphuncle communicates, of a far more extensive nature.

With respect to the pericardium itself, Professor Owen states, "The peritoneum, after lining the cavity which contains the crop and liver, and enveloping those viscera, forms two distinct pouches at the bottom of the pallial sac, in one of which, the left, is contained the gizzard, and in the other the ovary; anterior to these, and on the ventral aspect of the liver, is another distinct cavity, of a square shape, which contains the heart and principal vessels, with the glandular appendages connected therewith." This is what the author terms the pericardium.

As Van der Hoeven has pointed out, however, the gizzard lies to the right and the ovary to the left. Moreover, the gizzard is superior to the ovary, so as only to overlap it a little above; and I can find no evidence of the existence of such distinct pouches as those described.

Professor Owen states that the branchiæ "arise by a common peduncle from the inner surface of the mantle." My own observations, however, and Van der Hoeven's figures, of both male and female, lead me to believe that the peduncles of the branchiæ are perfectly distinct from one another.

The follicles of the branchial arteries are thus described in the "Memoir on the Pearly Nautilus:"—"They are short and pyriform and closely set together. To each of the branchial arteries are appended three clusters of these glands, of which one is larger than the united volume of both the others; and the larger cluster is situated on one side of the vessel and the two smaller on the opposite side. Each of these clusters is contained in a membranous receptacle proper to itself, partitioned off, as it were, from the pericardium, but communicating with it. . . . The two canals which form the communication between the pericardium and the branchial cavity commence at the receptacle of the lesser cluster attached to the superior branchial arteries, and terminate at the papillæ before men-

tioned, which are situated at the roots of the branchiæ. The pericardium and these receptacles of the glands, when first laid open, were found filled with a coagulated substance so closely compacted as to require a careful removal, bit by bit, before the contained follicles and vessels could be brought into view."

Like Valenciennes and Van der Hoeven, I have been unable to find any communication between the four sacs in which the small double clusters of follicles are contained, and the "pericardium;" and I hold it to be certain that the other four sets of follicles are not contained in sacs at all, but lie free in the "pericardium" or posterior chamber.

No notice is here taken of the widely different characters of the anterior and posterior follicles; and the figure gives both a similar structure.

Valenciennes ("Nouvelles Recherches sur le Nautile Flambé," 'Archives du Muséum,' ii. 1841) pointed out the existence of three pairs of apertures opening into the branchial sac, besides the genital and anal openings; and he affirms that they open into as many closed sacs, which communicate neither with one another nor with the cavity that contains the heart. M. Valenciennes indicates the difference in the structure of the anterior and posterior venous appendages. He seems to me to have seen something of the part which I have described as the pallio-visceral ligament; but I cannot clearly comprehend either his figure or his description.

Van der Hoeven, in his 'Contributions to the Knowledge of the Animal of *Nautilus pompilius*,' 1850, confirmed the statement of Valenciennes with regard to the existence of three pairs of apertures; but he showed, in opposition to him, that one of these pairs of apertures communicated with the pericardium. The sacs into which the other two pairs open are, according to this anatomist, blind. In the aperture of the anterior blind sac he found a concretionary matter which he supposed to contain uric acid, but chemical analysis did not confirm the supposition. Van der Hoeven refers to some observations by Vrolik; but as these are in Dutch, and have not, so far as I can find, been translated into either French, German, or English, I know not what they may contain.

In his more recent essay, translated in 'Wiegmann's Archiv' for 1857, under the title of "Beitrag zur Anatomie von *Nautilus pompilius*," Van der Hoeven states that he has again found hard concretions in the chamber enclosing the appendage of the anterior branchial artery, and that these on chemical analysis yielded phosphate of lime and traces of fat and albumen, but no uric acid.

Mr. Macdonald, in a valuable paper on the anatomy of *Nautilus umbilicatus*, published in the Philosophical Transactions for 1855, thus describes the follicular appendages of the branchial arteries:—

"These follicles are subcylindrical in form, somewhat dilated at the free extremity, to which is appended a folded and funnel-shaped process of membrane, which expands rather suddenly, presenting a jagged and irregular border. They open by a smooth and oval or slit-like orifice into the afferent pulmonary vessels, on each of which, as Professor Owen has observed, they are disposed in three clusters. The outer membrane is smooth and glassy, homogeneous in structure

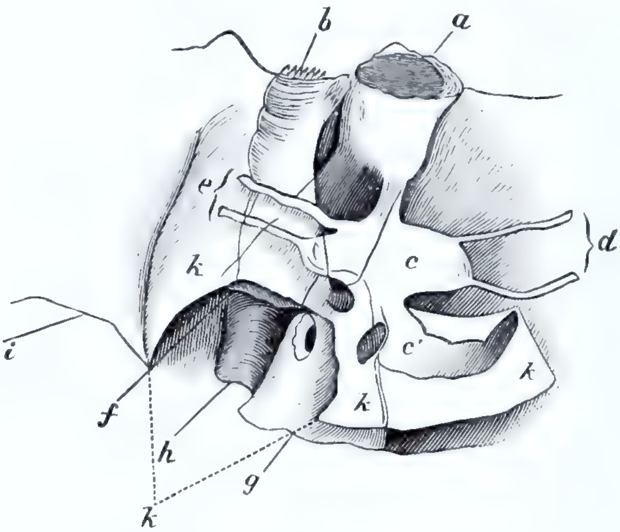


FIG. 2.—*Nautilus pompilius.* Natural size.

The pallio-visceral ligament seen from below: torn on the right side to show the rectum and oviduct; cut through on the left side along the dotted line close to *d'* in the preceding figure.

a. Anus. *b.* Oviducal aperture. *c.* Heart. *d.* Left branchial veins. *e.* Right branchial veins. *f.* Oviduct cut through. *g.* Ovary. *h.* Rectum. *i.* Mantle. *k k k.* Pallio-visceral ligament; *k'.* its torn portion. The oval "aperture for the siphonal artery" is seen to the left of *c'*, and the right-hand style in Fig. 1 passes through it.

and sprinkled over with minute rounded and transparent bodies, probably the nuclei of cells. Beneath this layer, flat bundles of fibres, apparently muscular, are traceable here and there, principally disposed in a longitudinal direction, and sometimes branched. The lining membrane consists of a loose epithelial pavement in many respects similar to that of the uriniferous tubules of the higher animals, the cells containing, besides the nuclei, numerous minute oil-globules, or a substance much resembling concrete fatty matter. This membrane is thrown up into an infinite number of papillæ and corrugations, so as to augment the extent of surface considerably.

The papillæ are more numerous at the inner part or towards the attached end; and a circlet of longitudinally disposed folds radiate from the bottom of the follicles, in which a number of small pits or fenestrations are sometimes visible. The sides of these folds are wrinkled transversely so as to present a median zigzag elevation. The funnel-shaped membranous process above noticed is continuous with the lining membrane, consisting of an extension of the same epithelial pavement; but the cells are somewhat larger and more regular in form. The cavity of each follicle, therefore, communicates with the exterior through the centre of this process; and the aperture is thus guarded by a kind of circular valve, permitting the escape of secreted matter, but effectually preventing the entrance of fluid from without."

In his fig. 9, pl. xv., Mr. Macdonald depicts certain "crystalline bodies often occurring within the follicles."

From what Mr. Macdonald states, one would be led to conclude that all the follicles have the same structure; but I suspect this to be an oversight.

In the second edition of Professor Owen's "Lectures on the Invertebrata" (1855), I find no mention of Valenciennes' discovery of the additional four apertures; but the author states that "on each side, at the roots of the anterior branchiæ, there is a small mamillary eminence with a transverse slit, which conducts from the branchial cavity to one of the compartments of the pericardium containing two clusters of venous glands. There are also two similar, but smaller, slits, contiguous to one another, near the root of the posterior branchia on each side, which lead to and may admit sea-water into the compartments containing the posterior cluster of the venous follicles." In this work the ovary is not only described, but *figured*, on the right side of the gizzard. The figure, however, rightly places the greater part of the ovary below that organ.

IV

ON THE PERSISTENT TYPES OF ANIMAL LIFE

Proceedings of the Royal Institution of Great Britain, vol. iii. 1858–62, *pp.* 151–153. (*Friday, June* 3, 1859.)

THE successive modifications which the views of physical geologists have undergone since the infancy of their science, with regard to the amount and the nature of the changes which the crust of the globe has suffered, have all tended in one direction, viz., towards the establishment of the belief, that throughout that vast series of ages which was occupied by the deposition of the stratified rocks, and which may be called "geological time" (to distinguish it from the "historical time" which followed, and the "pre-geological time," which preceded it), the intensity and the character of the physical forces which have been in operation, have varied within but narrow limits; so that, even in Silurian or Cambrian times, the aspect of physical nature must have been much what it is now.

This uniformitarian view of telluric conditions, so far as geological time is concerned, is, however, perfectly consistent with the notion of a totally different state of things in antecedent epochs, and the strongest advocate of such "physical uniformity" during the time of which we have a record might, with perfect consistency, hold the so-called "nebular hypothesis," or any other view involving the conception of a long series of states very different from that which we now know, and whose succession occupied pre-geological time.

The doctrine of physical uniformity and that of physical progression are therefore perfectly consistent, if we regard geological time as having the same relation to pre-geological time as historical time has to it.

The accepted doctrines of palæontology are by no means in harmony with these tendencies of physical geology. It is generally believed that there is a vast contrast between the ancient and the modern organic worlds—it is incessantly assumed that we are acquainted with the beginning of life, and with the primal manifestation of each of its typical forms: nor does the fact that the discoveries of every year oblige the holders of these views to change their ground, appear sensibly to affect the tenacity of their adhesion.

Without at all denying the considerable positive differences which really exist between the ancient and the modern forms of life, and leaving the negative ones to be met by the other lines of argument, an impartial examination of the facts revealed by palæontology seems to show that these differences and contrasts have been greatly exaggerated.

Thus, of some two hundred known orders of plants, not one is exclusively fossil. Among animals, there is not a single totally extinct class; and of the orders, at the outside not more than seven per cent. are unrepresented in the existing creation.

Again, certain well marked forms of living beings have existed through enormous epochs, surviving not only the changes of physical conditions, but persisting comparatively unaltered, while other forms of life have appeared and disappeared. Such forms may be termed "persistent types" of life; and examples of them are abundant enough in both the animal and the vegetable worlds.

Among plants, for instance, ferns, club mosses, and *Coniferæ*, some of them apparently generically identical with those now living, are met with as far back as the Carboniferous epoch; the cone of the oolitic *Araucaria* is hardly distinguishable from that of existing species; a species of *Pinus* has been discovered in the Purbecks, and a walnut (*Juglans*) in the cretaceous rocks.[1] All these are types of vegetable structure, abounding at the present day; and surely it is a most remarkable fact to find them persisting with so little change through such vast epochs.

Every subkingdom of animals yields instances of the same kind. The *Globigerina* of the Atlantic soundings is identical with the cretaceous species of the same genus; and the casts of lower Silurian *Foraminifera*, recently described by Ehrenberg, assure us of the very close resemblance between the oldest and the newest forms of many of the *Protozoa*.

Among the *Coelenterata*, the tabulate corals of the Silurian epoch

[1] I state these facts on the authority of my friend Dr. Hooker.

are wonderfully like the millepores of our own seas, as every one may convince himself who compares *Heliolites* with *Heliopora*.

Turning to the *Mollusca*, the genera *Crania*, *Discina*, *Lingula*, have persisted from the Silurian epoch to the present day, with so little change, that very competent malacologists are sometimes puzzled to distinguish the ancient from the modern species. *Nautili* have a like range, and the shell of the liassic *Loligo* is similar to that of the "squid" of our own seas. Among the *Annulosa*, the carboniferous insects are in several cases referable to existing genera, as are the *Arachnida*, the highest group of which, the scorpions, is represented in the coal by a genus differing from its living congeners only in the disposition of its eyes.

The vertebrate subkingdom furnishes many examples of the same kind. The *Ganoidei* and *Elasmobranchii* are known to have persisted from at least the middle of the Palæozoic epoch to our own times, without exhibiting a greater amount of deviation from the typical characters of these orders, than may be found within their limits at the present day.

Among the *Reptilia*, the highest group, that of the *Crocodilia*, was represented at the beginning of the Mesozoic epoch, if not earlier, by species identical in the essential character of their organization with those now living, and presenting differences only in such points as the form of the articular faces of their vertebræ, in the extent to which the nasal passages are separated from the mouth by bone, and in the proportions of the limbs. Even such imperfect knowledge as we possess of the ancient mammalian fauna leads to the belief that certain of its types, such as that of the *Marsupialia*, have persisted with no greater change through as vast a lapse of time.

It is difficult to comprehend the meaning of such facts as these, if we suppose that each species of animal and plant, or each great type of organization, was formed and placed upon the surface of the globe at long intervals by a distinct act of creative power; and it is well to recollect that such an assumption is as unsupported by tradition or revelation as it is opposed to the general analogy of Nature.

If, on the other hand, we view "Persistent Types," in relation to that hypothesis which supposes the species of living beings living at any time to be the result of the gradual modification of pre-existing species—a hypothesis which, though unproven and sadly damaged by some of its supporters, is yet the only one to which physiology lends any countenance—their existence would seem to show, that the

amount of modification which living beings have undergone during geological time is but very small in relation to the whole series of changes which they have suffered. In fact, palæontology and physical geology are in perfect harmony, and coincide in indicating that all we know of the conditions in our world during geological time, is but the last term of a vast and, so far as our present knowledge reaches, unrecorded progression.

V

ON THE STAGONOLEPIS ROBERTSONI (AGASSIZ) OF THE ELGIN SANDSTONES; AND ON THE RECENTLY DISCOVERED FOOTMARKS IN THE SANDSTONES OF CUMMINGSTONE.

Quarterly Journal of the Geological Society, vol. xv. 1859, *pp.* 440–460.

Plate XIV. [Plate 6].

Contents :—Introduction—Dermal Scutes of Stagonolepis—Dermal Scutes of Recent Crocodilia—Dermal Scutes of Fossil Crocodilia and Teleosauria—Comparison of the Scutes of Stagonolepis with those of Crocodilia and Teleosauria—Bones of Stagonolepis—Affinities of Stagonolepis—Footprints—Note (Postscript).

Introduction.—In establishing the genus *Stagonolepis* Professor Agassiz remarks[1]—"I have founded this genus upon a slab on which the impression of many series of great rhomboidal scales, arranged in the same way as those of the *Lepidosteidæ*, is observable. The angular form of these impressions allows of no doubt that the fish whence they proceeded was a great ganoid similar to *Megalichthys.* The absence of the fins, of the head, and of the teeth, however, renders the exact determination of the family to which the fossil belongs impossible. I arrange it provisionally in the neighbourhood of the genus *Glyptopomus*, to which it presents some analogy in the ornamentation of its scales."

Professor Agassiz goes on to say, in a subsequent paragraph, that the fossil came from the Upper Old Red at Lossiemouth; that he had not himself seen the original, and that he was acquainted with it only through Mr. Robertson's drawings.

Stagonolepis has remained ranged among the fishes in all the works on Geology and Palæontology which have been published since the appearance of the 'Monographie.' Sir C. Lyell, however,

[1] Monographie des Poissons fossiles du vieux grès rouge, p. 139.

informs me that some years ago, after perusing the memoir on *Mystriosaurus* by Dr. A. Wagner, to which I shall have occasion to refer by and by, his suspicions were aroused as to the real affinities of this so-called fish; and he even communicated to the late Mr. Hugh Miller his doubts (based on the strong resemblance which he perceived between the sculpture of the dermal plates of *Stagonolepis* and that represented by Dr. Wagner in the scutes of *Mystriosaurus*) whether, after all, *Stagonolepis* might not be a reptile. That eminent investigator of the Old Red Sandstone fossils was, however, so fully satisfied of the piscine nature of the remains that Sir Charles Lyell did not press his objections, and it might have been long before the question had been revived had not Sir Roderick Murchison been led to visit the Elgin country in the course of the present year (1858). On examining the bony remains associated with scutes of *Stagonolepis*, some of which were preserved in the Elgin Museum and in the collections of Mr. Patrick Duff and of the Rev. Mr. Gordon, while others were collected by himself, Sir R. I. Murchison was so impressed by their obviously reptilian characters that he used every exertion to gather together all the evidence which could tend to elucidate so important a question. In pursuing this object, Sir Roderick was aided in the most zealous and liberal manner by the Committee of Management of the Elgin Museum, by Mr. Patrick Duff, and by the very active personal exertions in the field of the Rev. George Gordon.

To the two latter gentlemen my own thanks are also especially due for their prompt courtesy in attending to the many inquiries and requests with which I have had to trouble them, since it became my duty, in accordance with the instructions of the Director-General of the Geological Survey, to enter upon investigation of these remains.

Thanks to these many helping hands and heads, that duty has been rendered far easier of performance than it promised at first to be, and I hope to exhibit to the Society to-night such an amount of evidence as will fully justify the conclusions I have to propound.

I would premise that, on the present occasion, I purpose to speak only of such portions of the ancient reptile—for such it truly is—as bear directly on those conclusions; and that the full description and illustration of all the remains which have been discovered will be reserved for the Memoirs of the Survey.[1]

[1] In order to render the following pages as useful as possible to the ordinary readers of the Journal, I have given a disproportionately full description, accompanied with figures, of the scutes and footmarks, as it is in these parts that the pure geologist is most likely to be interested.

The reptilian fossils from Elgin, which have passed through my hands, are of three kinds:—1st, Bones; 2nd, Natural casts of bones and teeth; 3rd, Footprints.

Of these, the first have been derived exclusively from the Lossiemouth quarries; the second are almost wholly from Findrassie; while the third class of remains is derived exclusively from Cummingstone. I am informed that up to the present time[1] no fossils referable to vertebrate animals have been found in either of these localities, save such as may with the highest probability be considered to belong to *Stagonolepis.*

Dermal Scutes of Stagonolepis (Pl. XIV. [Plate 6] figs. 1, 2, 3).—The first series of remains of which I purpose to speak are the dermal scutes and their casts.

Of these there are two kinds: the one distinguished by their flattened outer and inner surfaces and nearly square shape; the other, by having a bent or angulated contour arising from the possession of a longitudinal ridge externally, and of a correspondingly excavated inner surface. While the former, which, for distinction's sake, may be termed the *flat scutes*, preserve pretty nearly the same dimensions, the latter, or *angulated scutes*, vary greatly in size, some being very much larger, and others as small as, or even smaller than, the flat scutes.

The characteristic features of the *flat scutes* are best exhibited by the specimen upon which the genus was originally founded. It is very briefly described by Professor Agassiz, and is figured in pl. 31, figs. 13 and 14, of his already cited 'Monographie.' The specimen is an irregularly broken mass of sandstone, exhibiting numerous impressions of four-sided scutes, of which there are altogether five rows in one direction and eleven in the other. A plaster-cast (Pl. XIV. [Plate 6] fig. 1) shows, even better than the original, that, while one opposed pair, out of the four edges of each scute, fitted against the adjoining edges of the scutes on each side, the other pair of edges alternately overlapped, and were overlapped by, those of the adjacent scutes. There can be no doubt that the overlapped edges were anterior, and, as I shall presently show that these scutes formed part of the ventral armour of the animal to which they belonged, the direction and relations of each row become at once definable. The five rows are longitudinal—the eleven transverse. None of these rows are complete. The left-hand longitudinal row contains five scutes, whose outer (left) edges are more or less broken away. The next row contains seven scutes, the posterior of which are somewhat thrust

[1] See the concluding Note to this paper, p. 117.

forward, and their left edges somewhat broken. The third row contains eight scutes. Each of these longitudinal rows extends to the same level anteriorly; but the next, or fourth, series begins opposite the fifth scute of the third series, and but a very small portion of its first scute is visible. It contains six scutes, of which the hindermost are somewhat displaced and thrown forwards one upon the other. The fifth series contains only portions of five scutes, which are more or less displaced towards the right side.[1]

An additional small fragment of a scute is visible in front of the first and third series. Each scute is on exactly the same level as its right-hand and left-hand neighbour, so that the structure of the whole fragment is extremely regular.

About a fifth of the outer surface of each scute is covered by the posterior edge of its predecessor; and the fifth and sixth scutes of the fourth series are sufficiently displaced to show that the covered surface was smooth and bevelled off obliquely, so as to constitute a sort of articular facet, narrow and parallel-sided antero-posteriorly, but very wide transversely.

The posterior edge of this facet is cut perpendicularly to the plane of the scute, from whose face it rises like a kind of parapet. The face of the scute is ornamented with a peculiar sculpture, consisting of distinct deep pits. The casts of these are of course elevated, and lie like drops upon the general surface of the impression—an appearance which doubtless suggested the name of the genus. Near the centre of the face of the scute the pits are nearly circular in outline, but towards the periphery they elongate in the direction of radii from a point rather nearer the anterior than the posterior edge of the whole scute, and assume a pyriform shape, the small end of each being directed inwards. The consequence of this arrangement is a very marked radiation of the ornamentation from a centre which lies about the junction of the anterior two-fifths with the posterior three-fifths of the whole ornamented surface. A small marginal space, laterally and posteriorly, is, as Professor Agassiz has observed, free from sculpture (fig. 1).

An inch and a quarter transversely, by a little less antero-posteriorly, is a fair statement of the average dimensions of these flat scutes, of which I have only seen one or two detached impressions among the more recently discovered remains of *Stagonolepis*.

[1] I have applied the terms right and left here, not to the true right and left series or scutes, but to those which appear to be right and left when the face of the fossil is turned towards the observer and its anterior end is forward.

The *angulated scutes* may be roughly divided into three kinds: the *broad*, the *thick*, and the *irregular*.

The *broad angulated scutes* (fig. 2) have a transversely elongated trapezoidal form,—one of the short sides, which it will appear is the outer, not being parallel to the other, but sloping obliquely outwards and forwards. The largest of these scutes which I have seen is a well-preserved specimen from Lossiemouth, which, with the exception of a very small portion of its anterior and inner edge, is entire.[1] The anterior edge has a length of $4\frac{7}{8}$ inches; the posterior of $4\frac{3}{8}$ inches. The length of the scute in the middle line is $2\frac{1}{2}$ inches. The inner edge is straight; the outer, somewhat convex behind and concave in front, passes into the produced antero-external angle. The inner surface only of this scute was visible, but, by cutting away a portion of its substance, the ornamentation of the outer surface and its natural cast in the sandstone came into view, so that the relations of both surfaces could be observed. The contour of the outer surface is somewhat concave from before backwards, and the anterior edge of the scute is bevelled as in the flat scutes; the articular facet (*a*) thus formed is wider externally and internally than in the middle.

About $1\frac{5}{8}$ inch from the inner edge, and therefore much nearer the inner than the outer, a strong longitudinal ridge appears upon the scute, and, rising posteriorly, ends upon the hinder edge of the bony plate in a sort of rudimentary spine (*b*), while anteriorly it gradually dies away. The outer face of the scute falls away rapidly on each side from the ridge, so that, while measured through the ridge, the posterior margin of the scute is $\frac{7}{16}$ths of an inch thick, at a distance of three-quarters of an inch from it, on the outer side, it measures hardly more than $\frac{1}{8}$th of an inch, and is but little thicker at a like distance on the inner side.

The outer surface of this *wide angulated* scute is sculptured in the same way as that of the flat scutes, but the pits are larger, and the marginal ones are so much elongated as almost to deserve the appellation of grooves. The posterior, most prominent part of the ridge, is devoid of sculpture. The inner surface of this and of other scutes of the same order is quite smooth, except posteriorly, where it presents a fine transverse striation; and its contour is totally different from that of the outer surface. Transversely it is concave, each side sloping towards a longitudinal valley, which corresponds with the external ridge, and therefore lies altogether on the inner side of the

[1] I have since seen a specimen of one of these scutes $5\frac{1}{2}$ inches wide by $2\frac{1}{2}$ inches long.—July 5th, 1859.

middle line. The transverse concavity is least in the middle of the scute and greatest at its posterior edge.

Antero-posteriorly the inner surface is very convex in the middle line, its anterior and posterior moieties meeting in a rounded transverse ridge, which is nearer the anterior than the posterior margin. That part of the scute which lies behind this transverse boundary is much thicker than that which lies in front of it. None of the numerous wide angulated scutes which I have met with have been less than two inches in transverse diameter.

Of the *thick angulated scutes* to which I have referred, I know only the inner faces, and the minimum thickness, as no one of the specimens (which are all natural casts) shows the outer face. Again, the only specimens I have met with have been associated with remains belonging to the anterior part of the body, such as the scapulæ or the ribs.

A cast of one of these, on the same slab with the impressions of two scapulæ, is two inches long in the middle, and has the same width at its widest part, but it is not quite square. The side which I take to be the inner is nearly straight; and the inner edge, which is $2\frac{1}{6}$ inches long, appears to have been thick, and serrated for sutural union with its fellow. The anterior side measures about $1\frac{3}{4}$ inch in length, and is somewhat broken, so that its proper contour can hardly be made out. The junctions of the internal anterior and posterior edges appear to have been sharply angular, while the antero-external angle was slightly, and the postero-external angle greatly, rounded off. The internal surface is convex from before backwards, concave from side to side.

I have found scutes very similar to these, but smaller, associated with the impressions of some ribs. The smallest of these was not more than an inch long, and one which had a length of $1\frac{1}{2}$ inch was fully half an inch thick at its postero-external angle. On the other hand, scutes of this kind appear in some cases to have attained a width of more than four inches, and a thickness of seven-eighths of an inch.

The *irregular angulated scutes* (fig. 3) are pentagonal or rhomboidal, the ridge by which they are marked externally projecting so far backwards that their posterior margin (*b*) becomes triangular. One of the largest of these had a length of $1\frac{7}{8}$ inch by a breadth of half an inch, and had a roughly pentagonal form, its anterior edge being slightly convex. Another had a length of $1\frac{1}{2}$ inch by a breadth of $\frac{5}{8}$ths of an inch, and presented only a very small sculptured surface close to its anterior margin. In fact, the proportion of the

sculptured to the smooth surface was far less in these than in the wide scutes.

I have compared the parts which have just been described with the scales of *Glyptopomus*; and, though there is a certain resemblance between the latter and the flat scutes, the dermal plates of no fish with which I am acquainted present any similarity to the angulated and thick scutes. On the other hand, any one acquainted with the characters of the exoskeleton in the Crocodilian Reptiles can hardly fail to have his attention arrested by the remarkably similar features of the scutes of *Stagonolepis*; and close investigation shows that there is not a single peculiarity of the latter which may not at once be paralleled by those of Crocodilian scutes. To begin with the sculpture or ornamentation,—the outer surface of the scutes exhibits distinct rounded pits, so disposed as to appear to radiate more or less distinctly from a common centre, not only in the modern Crocodiles, but in the Eocene *Crocodilus Hastingsiæ* and in the Mesozoic *Teleosauria*. Wherever these scutes possess a median ridge, the centre of radiation of the pits is somewhere on that ridge, and the highest part of the ridge is devoid of sculpture. Next, in respect of their form—the variously-shaped scutes of *Stagonolepis* become readily intelligible when those of the existing and extinct *Crocodilia* are understood. To this end, however, I must here interpolate a brief disquisition upon the characters of the dermal armour in the *Crocodilia* in general,—a subject upon which I have not found it very easy to gain definite information.

Dermal Scutes of Recent Crocodilia.—So far as my present information goes, there are two modes of arrangement of the dermal armour among the *Crocodilia*—the one characteristic of the recent Crocodiles, the other known to exist in the Amphicœlian genera. In the recent *Crocodilia* there are numerous longitudinal series of dermal plates upon the dorsal region of the body. The large and regular scutes are divisible into three distinct sets: nuchal, cervical, and dorso-caudal. The scutes do not always overlap, and in the dorsal region there may be as many as ten regular and large scutes in a transverse row. Along the margins of the shield formed by the regular scutes small and irregular ones are scattered.

The ventral armour varies greatly, no osseous plates at all being developed in this region in some recent *Crocodilia*, while in others I find the ventral shield to be very largely developed.

In the Amphicœlian *Crocodilia*,[1] at any rate in the *Teleosauria*,

[1] The scutes of the specimen of *Goniopholis crassidens* in the British Museum exhibit a narrow smooth articular facet along that edge which is produced into the peg; but I am

the disposition of the dermal armour, as will be shown below, is very different. The most numerous scutes are on the ventral surface of the thorax and abdomen, where they form six longitudinal, and as many as twenty transverse rows. In the dorsal region, on the other hand, no distinct nuchal and cervical scutes have as yet been discovered; and in the dorso-caudal regions, the scutes, which are occasionally very large, and are usually broad in proportion to their length, never form more than two longitudinal rows, the scutes of each row being suturally united in the middle line, and free at their outer edges. There is no evidence of the existence of any scattered small scutes, or that anything but soft parts united the dorsal with the ventral shield.

Such are the chief modes in which the dermal armour of the *Crocodilia* is disposed. With respect to the form and mode of union of the component scutes, it does not appear that many general rules can be laid down. The scutes are, however, always disposed symmetrically with regard to the median planes of the back and belly, in such a manner that the middle line answers to the interval or suture between two longitudinal rows of scutes.[1]

The dorsal scutes almost always present a more or less marked longitudinal ridge externally, while the ventral scutes, when they exist, have either flat and smooth, or evenly curved external surfaces.

In some procœlian recent *Crocodilia*, such as *Crocodilus acutus*, there are no ventral osseous scutes. The dorsal scutes, on the other hand, are well developed; they are either square, pentagonal, or hexagonal, and their lateral edges are very irregular and jagged. I cannot find in any case, however, that they interlock so as to unite suturally,—a greater or less portion of the dermis being in all cases interposed between their edges. The scutes nowhere overlap, and, as might be expected, they exhibit no articular facets.

Each scute presents externally a strong longitudinal ridge, which lies on the outer side of the median line, and cuts the hinder margin of the scute posteriorly, while anteriorly it subsides into the general

not aware that there is any evidence to show whether these scutes were dorsal or ventral, or in what manner they were arranged. Their sculpture consists of distinct pits; but the peripheral pits are not particularly elongated, and hence there is no marked appearance of a radial arrangement.

[1] The only exceptions to this rule that I am acquainted with are offered by the scutes of the median caudal crest, and by a small extent of the dorsal region of the tail, just in front of the point of convergence of the lateral crests. Here there is a variable number of scutes, which lie one behind the other, gradually diminishing in size, in single series, so that their centres correspond with the median line.

surface at some distance from the anterior margin. The highest point of the ridge is far nearer the posterior than the anterior margin.

The inner faces of the scutes are smooth, concave from side to side, and slightly convex from before backwards.

Scattered about between the ventral and cervical, and the cervical and dorsal shields, there are many small and irregular detached scutes, of all sizes down to $\frac{3}{8}$ths of an inch in length. The smallest of them are simply incipient ossifications in the dermis which underlies the ridges of the epidermic scales, and they present no sculpture. In fact they correspond with the apices of the ridges of the larger scutes. In some of larger size, which present a certain amount of sculpture, the apex of the ridge is altogether posterior, and the scutes very closely resemble the smaller *irregular angulated* scutes of *Stagonolepis*.

Other existing procœlian *Crocodilia* present a far more complete dermal armour; and certain Alligators, of the genus or subgenus *Jacare*,[1] are not surpassed, so far as I am aware, by any recent *Crocodilia*, and certainly not by any of the fossil members of the group; though Cuvier calls *Teleosaurus Cadomensis* "le mieux cuirassé" of the group to which it belongs. I shall describe the dermal skeleton of the *Jacare* at length in another place; but I may remark here, that the broadest part of the dorsal shield exhibits eight or ten scutes in each transverse row, and that all the dorsal scutes overlap their successors by their posterior edges, and are united to one another by strong serrated sutures. The ventral shield consists, in its broadest part, of 12–14 scutes in a transverse row. Each scute, except the two outermost of the series, has four straight sides, the anterior of which presents a large, smooth, articular facet, while the posterior overlaps the facet in its successor. The lateral edges unite in firm serrated sutures. The outer faces of these scutes are quite flat, and their ornamentation is so very similar to that of the *Stagonolepis*, that it would require very close attention to distinguish a cast of the one from a cast of the other. Multitudes of small, irregular, posteriorly pointed, osseous scutes cover the skin of the sides of the body, and extend on to the limbs.

Dermal Scutes of Fossil Crocodilia and Teleosauria.—Among the

[1] *Alligator lucius*, like *Crocodilus vulgaris*, has no ossified ventral scutes. *Caiman palpebrosus* has ventral scutes like those of *Jacare*, of which I have examined two species, *J. fissipes* and *J. sclerops*. I have nowhere been able to find the slightest allusion to the existence of this singularly developed ventral armour in modern *Crocodilia*. (See concluding Note, p. 117.)

fossil procœlian *Crocodilia*, the scutes of *Crocodilus Hastingsiæ* are provided with articular facets, and I am inclined to think that this Crocodile also had a ventral shield.

With regard to the Amphicœlian Crocodiles, the broad statement I have made above must be held at present to apply only to the *Teleosauria*, and naturalists in general do not seem to have admitted its truth even for them. Cuvier, for instance, remarks, with regard to his "Crocodile de Caen" (*Teleosaurus Cadomensis*, Geoffroy), "They are rectangular and very thick, but are thinned towards their edges, and the whole of their external surface is excavated by little, close-set, hemispherical fossæ, of the size of a lentil or that of a pea. . . . . These scales were disposed, as in our living Crocodiles, in regular series, longitudinally as well as transversely. The posterior edge of the one covered the base of that which followed it. The block belonging to the Caen Academy presents almost all the scales of one side in their natural position. It is seen that, from the first of the dorsal vertebræ which have been preserved to the origin of the tail, there are 15 or 16 transverse series, and that each series had five scutes on each side, so that there were at least ten longitudinal series."[1]

The "Grand bloc de l'Académie de Caen," here referred to, is figured in Cuvier's plate 235, fig. 14. The scutes represented are all flat, four-sided, and nearly square, and their internal surfaces only are represented. Moreover, the figure clearly shows six longitudinal rows, and not five. I have no doubt that the scutes figured did in fact form a part of the ventral armour, and not, as Cuvier supposed, of the dorsal shield. I am the more inclined to adopt this opinion because Geoffroy St.-Hilaire, to whom we are indebted for the first accurate description of the dermal skeleton of the Teleosaurians, and who had the opportunity of examining all the specimens described by Cuvier, writes thus, without referring to Cuvier's statement:—

"In the Teleosaurians it is the ventral plastron which is the more complete. It is protected by numerous contiguous series of six strong thick scales, which are flat and imbricated at their posterior edges. Upon the back there are indeed other larger scales, but they are only two in number in each row; bent scales exist only on the upper part of the tail."[2]

Dorsal Scutes.—As the Tesson Collection has recently been purchased for the British Museum, some of the specimens on which

[1] Ossemens Fossiles, vol. v. part 2, pp. 139, 140.

[2] Mémoires de l'Académie, vol. xii. p. 24.

Geoffroy made his observations are probably to be seen there. At any rate, the beautifully preserved remains of *Teleosaurus temporalis* and *T. Cadomensis*, in that collection, fully bear out his statements. In these *Crocodilia* (and I may add in *T. Bollensis* in the same collection), the dorsal scutes are arranged in only two longitudinal series, or, in other words, there are only two scutes in the successive transverse rows, which occupy the middle of the dorsal region. In *T. Cadomensis*, it is clear that each pair of scutes corresponds with a vertebra; and the posterior two-thirds of the broad terminal face of the short and thick spinous process is so shaped that the interior faces of its appropriate pair of scutes seem to have rested upon and have been closely connected with it. The internal edge of every scute is thick, and interlocks with its fellow by strong serrations. The suture thus formed lies in the middle line. The anterior edge, presents a broad articular facet, overlapped by the posterior edge of the preceding scute; the posterior edge thins out to overlap its successor. The outer edge also thins out, and neither its upper nor its under surfaces present the least trace of overlapping, or being overlapped by, or articulating with, other scutes.

Dr. A. Wagner,[1] who has given a very good account of the dermal armour of *Teleosaurus Cadomensis*, finds only two longitudinal rows of dorsal scutes, either in this species or in *Mystriosaurus Muensteri*. Bronn and Kaup[2] figure only two longitudinal series of dorsal scutes in their *Pelagosaurus typus*; and I can nowhere find the least evidence that the dorsal scutes were connected by anything more than the general integument with the lateral or ventral scutes.

Professor Owen[3] admits the existence of a double row of large or peculiarly formed medio-dorsal scutes in *Teleosaurus Chapmanni*; but he evidently conceives, from the following passage, that the lateral scutes were directly articulated with the dorsal ones, so that the body was surrounded by continuous circles of bony plates:—

"The verticillate cuirass of these ancient Crocodiles is thus securely braced round the trunk by this interlocking of the inferior extremities of each ring of scutes, whilst the imbricated arrangement would allow of a certain sliding motion of the rings upon each other, sufficient for the expansion of the chest in breathing."

No evidence is produced in favour of the existence of a structure

[1] Abhandlungen über die Gavial-artigen Reptilien der Lias-Formation, 1842.

[2] Die fossilen Ueberreste Gavial-artigen Saurier aus der Lias-Formation in der k. paläontologischen Sammlung zu München. Abhandlungen der Mathem.-Physikalischen Classe der Königlichen Bayerischen Akademie der Wissenschaften, Bd. v. 1850.

[3] Report on British Fossil Reptiles, Rep. British Assoc. 1841.

so aberrant from that of the other Teleosaurians, and it seems to me that, in leaving an interspace between the dorsal and ventral shields, nature has provided for the wants of the economy in a far more efficient manner than that here imagined.

Ventral Scutes.—The characters of the ventral armour of the *Teleosauria* are beautifully displayed in the two specimens from the Tesson Collection, of *Teleosaurus temporalis* and of *T. Cadomensis*, to which I have referred. The ventral shield is, in the latter case, incomplete; but the scutes are imbedded undisturbed in the rock. In the *Teleosaurus temporalis*, on the other hand, the shield is nearly complete, but all the parts have been artificially fitted together upon a plaster-slab; by whose hand I know not. The comparison of the two specimens, however, leads me to believe that the operation has been very carefully and conscientiously effected.

In *Teleosaurus temporalis* the scutes are so arranged that the middle line is occupied by the suture between the two innermost rows, and that there are three longitudinal rows on each side. Anteriorly, the innermost scutes are nearly square, while posteriorly they become pentagonal, or even hexagonal. The scutes of the two outer rows on each side are also nearly square anteriorly, but more or less completely hexagonal in the posterior part of the shield; and, from the manner in which the scutes are fitted together, the result is, that, while the anterior transverse rows are nearly or quite straight, the posterior ones form an angle, open forwards on each side of the middle line, so that each of the hinder rows assumes somewhat the form of a W.

There are altogether twenty transverse rows of scutes. Those of the last row do not exist in the specimen, but, from the outlines on the plaster, were evidently thought by its restorer to be smaller than those which preceded them, and to be so arranged as to give a rounded posterior margin to the ventral shield. Anteriorly, also, the scutes are partially wanting; but the transverse rows appear at first to have had not more than half their greatest width, and the anterior five rows seem to have contained only two scutes on each side of the median line. The shield does not attain its full width before the tenth series.

The lateral edges of the scutes are united by serrated sutural edges. The anterior edge of each exhibits a bevelled articular facet, occupying nearly a third of the whole external surface, and overlapped by a corresponding extent of the posterior margin of the preceding scute. Both surfaces of these scutes are smooth and flat, and the pitted sculpture radiates from a point which nearly cor-

responds with the centre of each scute, in a fine specimen of a fragment of the ventral shield of *Teleosaurus Cadomensis* (32,591 B.M.). The external scutes on each side are somewhat bent up towards the dorsal surface; but in this, as in other specimens, the outer margins of these scutes thin out, and exhibit not the least sign of having been connected with any other. In this respect there is a marked contrast between the outer and the inner edges.

There are six longitudinal rows in this specimen, which is the number assigned by Geoffroy St.-Hilaire (*supra*, p. 103) to the *Teleosauria* generally. Six exist, as we have seen, in *T. temporalis*. Dr. Wagner found only five in his specimens of the ventral shield of *T. Cadomensis*; but, as he states, it was imperfect. Six are, as I have pointed out, represented by Cuvier in *T. Cadomensis*, and the same number is shown in the figure, given by Bronn and Kaup, of *Pelagosaurus typus*. These authors state that there are ten longitudinal rows of scutes in the dermal armour of *Mystriosaurus longipes*; but their figures and description make me think that this is a hypothetical conclusion, and that what they have seen and figured is only the ventral armour, with its six rows of plates.

I cannot ascertain from Professor Owen's description what is the precise number of longitudinal series of "lateral and ventral" scutes in *Teleosaurus Chapmanni*. They are said to be "more perfect squares than those next the spine," and to have no keels. In these respects they obviously agree with the corresponding scutes of the *Teleosauria*; but it is stated that "the median abdominal scutes are not opposite but alternate; their median margins are rounded off or slightly angular; and, while the anterior part of that margin is overlapped by the posterior half of the opposite scute in advance, the posterior half overlaps the succeeding scutum of the opposite side." This description would apply much better to the sutures between a median series and that which follows it externally, than to the junction between the two median series of scutes, which are always opposite in the *Teleosauria* I have examined.

The internal faces of the dorsal scutes of the *Teleosauria* are concave from side to side, and convex from before backwards; they may be smooth or carinated, but the ventral scutes appear to be always flat and without a keel.

Comparison of the Scutes of Stagonolepis with those of Crocodilia and Teleosauria.—Bearing in mind the features of the dermal armour of the *Crocodilia* which have just been detailed, it becomes no difficult matter at once to find an analogue for each kind of scute found in *Stagonolepis*. The *flat scutes* are strictly comparable to those of the

ventral shield of the *Teleosauria*, the *broad* and the *thick angulated scutes* to the dorsal scutes of the same Crocodilians, while the *irregular angulated scutes* are very similar to the dermal bones, which are scattered between the margins of the dorsal and cervical shields of the existing Crocodiles.

At this stage of the inquiry, the full meaning of a piece of evidence, whose value I had, up till then, but very imperfectly recognized, became obvious. This was a remarkable natural cast, obtained by Mr. Patrick Duff, at Findrassie, and which had been sawn through longitudinally by that gentleman's direction, so as to expose its internal conformation. At first sight this curious fossil resembled nothing so much as the crushed and distorted cast of an *Orthoceras*, but both Mr. Duff and Sir Roderick Murchison had suspicions of its real nature, and in fact it turns out to be one of the most singular organic remains ever discovered, consisting of a natural cast of both the dermal bones and the vertebræ of a considerable segment of the tail.

Loaded by its heavy dermal plates, this caudal fragment appears to have sunk into the fine siliceous mud, the accumulation of which has given rise to the Findrassie sandstone, and to have been completely permeated therewith, all the cavities left vacant by the putrefaction of the soft parts becoming filled up with a substance which soon hardened into stone. After this had taken place, the bony matter was, by some agency or other (probably the percolation of water), completely removed, so that the fossil, which must have originally lain loose in a natural mould of the outer surfaces of the caudal scutes (which has unfortunately not been preserved), exhibits, externally, a complete cast of the inner surfaces of a number of successive transverse series of scutes, and, internally, the casts of the outer surfaces and neural canals of a corresponding number of caudal vertebræ.

The impressions of the dorsal scutes are but little disturbed, and it is at once obvious that they belonged to the kind which I have named above *broad angulated scutes*. They form a double series along the dorsal region of the tail, and their inner edges meet along a median sutural line.

The ventral scutes also appear to have formed only a double series, meeting in the middle line; but they are much more displaced, the left-hand set being particularly thrown out of position. These scutes are nearly square, and perfectly flat, corresponding exactly in form with the *flat scutes* already described. It would appear that in the caudal region (as was probably the case in the

Teleosauria) the outer margins of the dorsal and ventral shields came into close contact.

By the discovery of the true nature of this fragment, the conclusions to which the structural characters of the different kinds of scutes pointed were completely verified, and I had thenceforward no hesitation in assuming that *Stagonolepis* was provided with a dorsal and a ventral dermal shield, composed of scutes resembling those of *Jacare*, *Caiman*, *Crocodilus Hastingsiæ*, and the *Teleosauria*, in the manner in which their anterior and posterior margins are articulated together.

With respect to the mode in which the scutes were arranged to form the ventral and dorsal shields, *Stagonolepis* would appear to have resembled the *Teleosauria*. The fragment of the ventral shield which I described first is extremely like a portion of the anterior region of the ventral shield of a *Teleosaurus*, and it will be observed that it only contains five longitudinal rows of scutes.

On the other hand, all the impressions of the *broad* and *thick angulated scutes* which I have met with have one lateral margin straight, and apparently fitted for sutural union with the corresponding margin of another scute, while the other margin is rounded off, and is either thin, or, if thick, shelves off rapidly to a thin edge. Hence I conclude that these dorsal scutes formed, as in the *Teleosauria*, only a double series, and that their external edges were not, except perhaps in the caudal region, connected with other scutes.

The *irregular angulated scutes* only remain to be accounted for. They have much resemblance to the small scutes which are scattered along the margins of the great dorsal shield of existing Crocodiles; but it is possible they may have belonged to the narrower part of the tail.

To sum up in a few words the result of this long inquiry, it is evident that, in its dermal armour, *Stagonolepis* is altogether a Crocodilian Reptile.

Bones of the Stagonolepis.—I will abstain, at present, from particularly describing the impressions of ribs, of two scapulæ, and of the posterior face of the second sacral vertebra of *Stagonolepis*, because all these parts nearly resemble the corresponding bones of ordinary *Crocodilia*. Had my acquaintance with the organization of the Elgin reptile been confined to the remains already mentioned, in fact, I should have been fully justified, according to the ordinarily accepted canons of paleontological interpretation, in prophesying that any other parts which should be brought to light would conform very closely to the Crocodilian, and especially the Teleosaurian type. It

was a useful warning, however, to find that I should have been unsupported by the event, had I done so; for all the other remains depart, more or less widely, from the ordinary Crocodilian type of organization. The smallest amount of difference is perceptible in the femur, an incomplete cast of part of the shaft and distal end of which bone (of the left side) shows that it was thicker and stouter in proportion than that of the Crocodile. The impressions of the articular surfaces of the condyles, again, are so rough and irregular as to lead to the suspicion that they were covered by imperfectly anchylosed epiphyses—which is the reverse of a Crocodilian character.

The cast of the only example of a metacarpal or metatarsal bone which has come to light also exhibits proportions which indicate a much shorter and thicker foot than the corresponding bone in the modern Crocodiles, and, *à fortiori*, than in the *Teleosauria*. The proportions of these bones, then, lead us to look for a stouter thigh and a shorter and broader foot than exist in the *Crocodilia*. On the other hand, the single natural cast of a long and nearly straight bone, which I can only regard as an ungual phalanx, indicates a length of claw wholly foreign to the Crocodilian foot.

The vertebræ, whose more or less perfect natural casts have passed through my hands, all belong either to the dorsal, the sacral, or the caudal series. The impression of part of a sacral vertebra, to which I have already alluded, shows that in this region the structure of *Stagonolepis* was very similar to that of known *Crocodilia*; but the dorsal and caudal vertebræ are remarkable, partly for the lateral constriction and inferior excavation of their centra, partly for the obliquity of the planes of their slightly concave anterior and posterior articular faces. These faces, in fact, are not perpendicular to the longitudinal axis of the centrum, but the anterior one looks a little downwards and forwards, the posterior, upwards and backwards.

The neural arches were readily detached from their centra, and, where a separation has taken place, the previously co-adapted surfaces of the centrum and the arch exhibit strong ridges and grooves, which mutually interlock. The edges of the posterior zygapophyses meet inferiorly above the neural canal (which is deepest in the middle), forming a kind of inverted V.

These and some other peculiarities of the vertebræ of *Stagonolepis* are all shared by the *Teleosauria*, and may be readily seen in many of the detached Teleosaurian vertebræ in the British Museum; but the vertebræ of the reptile under description present two remarkable

characters, for which I can find no exact parallel in either recent or fossil *Crocodilia*.

The first of these is exhibited by each of two imperfect natural casts of anterior dorsal vertebræ, the strong and broad transverse processes of these vertebræ being bent upwards and backwards at an angle of 45° to a horizontal or vertical plane. The second peculiarity is exhibited by the caudal vertebræ, whose transverse processes come off altogether above the neuro-central suture, whereas ordinarily they are, as it were, wedged into this suture, and separate the centrum more or less completely from its neural arch.

With regard to the first of the special characters here noted, it may be observed that the anterior dorsal vertebræ of different species of modern *Crocodilia* vary a good deal in the extent to which they incline upwards and backwards, and those of some *Enaliosauria* suffer a still more marked deflection in the same direction; but it is among the Dinosaurian reptiles that the transverse processes of the dorsal vertebræ take a direction most nearly corresponding to that which obtains in *Stagonolepis*. Without attaching too much weight to this circumstance, it will be seen by and by that it is worth while to bear it in mind.

The second peculiarity to which I have directed attention may perhaps be the result of the early anchylosis of the caudal transverse processes with the neural arches. However this may be, the character in question is a very exceptional one, and long led me to hesitate in regarding the vertebræ in question as really caudal.

The gradual divergence from the strictly Crocodilian type of organization which is manifest in the remains to which I have just adverted reaches its climax in the next part I have to mention.[1] A fragment of bone protruding from the surface of one of the blocks of sandstone from Lossiemouth was the last to attract my attention of all the fossils which have been sent from Elgin. Certain indications convinced me that, notwithstanding the extreme fragility of the bony substance and the depth to which it seemed to penetrate into the sandstone, it was worth some trouble to work out this bone completely, and having succeeded, by dint of careful chiselling, in removing a considerable quantity of superincumbent matrix without damage to the fossil, I was rewarded by the view of the nearly entire ventral face of a coracoid bone, of a form very unlike what might have been anticipated. For this bone, far from having the transversely elongated form more or less constricted in the middle, which is exhibited by the corresponding part in all the true *Crocodilia* with

[1] See the final Note, p. 117.

which I am acquainted, whether mesozoic, cainozoic, or recent, is almost elliptical in outline, and the long axis of the ellipse, which is nearly parallel with the middle line, is to the short transverse axis as 6 to about 4. The articular surface for the humerus is crushed and partly broken away, and a part of the anterior external edge is incomplete. The posterior edge of the bone presents a deep excavation close to the articular end; and, if two lines were drawn, one longitudinally through the deepest part of the notch, and the other transversely through the greatest transverse diameter of the bone, they would cut one another in the midst of a circular foramen, which corresponds with the coracoid foramen of Crocodiles and many Lizards. I find no coracoid so similar to this as that of *Hylæosaurus*.[1]

Jaw and Teeth.—The only remaining fossil which bears strongly upon the question of the affinities of *Stagonolepis* is the impression of a fragment of what I conceive to be the lower jaw, exhibiting the remains of some eight or nine alveoli. The impressions of the teeth contained in four of these, situated near the anterior end of the fragment (which may or may not have been its natural termination), are tolerably perfect. The third tooth is the largest, though, judging by its alveolus, the fourth, which is wanting, must have been larger than even the third. The second tooth is emerging from the jaw, not more than half its length being visible beyond the alveolar edge.

The impression of the surface of the jaw is, though imperfect, an inch and a half deep in some places, while the longest tooth projects two and a quarter inches beyond the alveolar margin; so that this tooth was probably at least three inches long, while its greatest transverse diameter amounts to very little less than five-eighths of an inch.

The upper third of each tooth is slightly recurved, and the apex appears to have been lancet-shaped when young, but more obtuse and rounded afterwards. At the apex and for some distance below it (half an inch in the longest or fourth tooth) the surface of the tooth is smooth and polished, but further down numerous longitudinal ridges, with rounded surfaces, separated by very narrow grooves, make their appearance, and increase slightly in strength down to the alveolar margin. As might be expected from the subcylindrical figure of the tooth, the ridges do not increase in width towards its root.

The teeth appear to have had broad anterior and narrow posterior

[1] See concluding Note, p. 117.

faces, but there is no evidence that they possessed any definite cutting edge. The manner in which the teeth are crushed and cracked towards their alveolar ends indicates the existence of a large pulp-cavity, bounded by comparatively thin walls.

The alveoli are quite distinct from one another. The bony substance of the jaw has left such an impression as leads to the belief that it must have had a coarsely fibrous structure, more like that of a fish than that of a reptile. There is also a remarkable irregularity and want of parallelism about the disposition of the teeth, the fifth being greatly inclined backwards, and the second having a similar, though less marked, obliquity.

There is no positive proof that this fragment of a jaw belonged to *Stagonolepis*; but, as I have already stated, no vertebrate remains save those of this reptile have hitherto been found in the Findrassie quarry, whence the specimen was obtained, and the external characters and mode of implantation of the teeth are wholly unlike those of any of the large, probably piscine, teeth (of *Dendrodus*, *e.g.*) which have been discovered in the neighbouring beds of the Old Red Sandstone. (See the final Note, p. 117.)

If this jaw belonged to the same animal as that to which even the largest of the vertebræ which have been discovered belonged, the size of the teeth is remarkable, for the longest is considerably more than twice as long as the centrum of such a vertebra. On the other hand it must be recollected that the teeth of some of the ancient *Teleosauria* are extremely long in proportion to the jaw, and in other respects present resemblances to those contained in the fragment just described; while it is also possible that this fossil may have formed a part of an individual larger than any of those whose vertebræ have as yet come to light. As the evidence stands at present, I see no reason to doubt that the jaw belonged to *Stagonolepis*.

Assuming that *Stagonolepis* had the same general proportions as a Crocodile—as, from the characters of the jaw, femur, and caudal vertebræ, we have every reason to believe was the case—the largest remains I have met with, excluding the jaw just mentioned, indicate an animal about eight feet long. (See Note, p. 171).

Affinities of the Stagonolepis.—With regard to the affinities of the Reptile whose leading structural peculiarities have been detailed in the foregoing pages, I think it is clear that *Stagonolepis* is, in the main, a Crocodilian Reptile. Its dermal armour, its sacrum, its scapulæ, are eminently crocodilian; its femur and dorsal and caudal vertebræ are also crocodilian, though presenting small aberrations from the pure type. The teeth, though more divergent, are croco-

dilian in their mode of implantation and some other respects. The coracoid, on the other hand, is lacertilian or dinosaurian;[1] and, finally, if one may safely judge from the few remains which have hitherto presented themselves, the bones of the feet were neither crocodilian nor dinosaurian nor lacertilian.

I am at a loss to find an exact parallel for this peculiar combination of characters in any group of recent or fossil *Reptilia*. Among the Tertiary and recent Reptiles I know of nothing at all like it; and all the mesozoic *Crocodilia* with whose dermal armour that of *Stagonolepis* exhibits such a close resemblance, present no important divergence from the typical crocodilian structure of the coracoid, while their slender feet have undergone the opposite modification to that which appears to have taken place in *Stagonolepis*. The *Enaliosauria* and *Pterodactylia* afford us no terms of comparison; and from the *Dinosauria*, with which *Stagonolepis* presents one or two similarities, it is broadly separated by the especially crocodilian characters of its scutes and sacrum. These characters equally separate it from all the Triassic and Permian *Reptilia* which have hitherto been described. What little we know, at present, of the laws by which the distribution of life in past time was governed, does not seem to me to enable us to deduce from the existing data any conclusion as to the precise age during which the Elgin Reptile lived. Such a combination of characters as it presents would, I apprehend, be in perfect keeping with the known Reptilian Fauna of any epoch from the Wealden downwards.

Footprints (Pl. XIV. [Plate 6] figs. 4 and 5).—I have intentionally deferred to the end of my communication the description of the footmarks which have been observed upon the sandstones of Cummingstone, because, although they are certainly the tracks of Reptiles, there is, strictly speaking, no proof whatsoever that they were produced by the particular Reptile *Stagonolepis*, no fragment of which has been detected in the Cummingstone quarries. It is desirable therefore that the footmarks should be considered quite independently, though it may be instructive to inquire what positive and negative evidence there is in favour of thinking them to be the work of *Stagonolepis*.

Although a considerable series of these tracks has passed under my inspection, I have only seen two footmarks which are so clear and distinct as to satisfy my mind that they fairly represented the figure of the foot. The two impressions in question form part of a continuous track, evidently made by the same animal, and exhibiting

[1] See the Note p. 117.

three pairs of right-foot prints (of the fore and hind foot on each side) and two pairs of left-foot prints.

(*Fore Foot.*)—The most distinct impression of the anterior foot (fig. 4) is the middle one of the three on the right side. Its greatest breadth is $2\frac{3}{4}$ inches, its greatest length $3\frac{3}{4}$ inches. The plantar surface of the foot measures $1\frac{1}{2}$ inch in its greatest anterior-posterior diameter. The impressions of five digits are visible; and the proximal joints of the third digit, taken together, equal rather more than an inch in length, while the impression of its terminal joint is $1\frac{1}{4}$ inch in length.

This plantar impression is on the whole transversely oval, its anterior boundary presenting a tolerably even convexity forwards, while the posterior boundary, equally, or more, convex backwards, presents an emargination opposite the base of the middle digit. A line drawn from the emargination to the base of the fourth digit would divide the plantar impression into a shallow outer portion and a more deeply concave inner portion. A line drawn from the emargination to the interspace between the first and second digits, again, would divide the concave inner surface into a deeper external portion and an internal portion, the latter gradually shallowing towards the inner side, and passing into the impression of the inner digit, which diverges so much from the direction of the others, and seems to have been comparatively so thick and short, that it might well be termed a thumb. The proximal portion of this thumb seems at first to terminate in a strong curved impression convex outwards and forwards, and deepest internally, which has somewhat the shape of a comma set transversely (‿).

The distance from the emargination to the end of this impression is $1\frac{7}{8}$ inch; beyond it is an interval of $\frac{3}{8}$ths of an inch; and then follows a shallow longitudinal mark, $\frac{3}{4}$ inch long and nearly $\frac{1}{4}$ inch broad, which takes a direction nearly parallel with that of the ungual phalanges of the other digits, and terminates opposite the base of the ungual phalanx of the second digit.

The last-mentioned features are only to be made out by examining the tracks very carefully by artificial, or by very oblique natural, light.[1] Whether, as I originally supposed, the deep comma-shaped impression is the mark of a nail covering the second phalanx, or whether it has been produced by the first phalanx,—the longitudinal mark being the true impression of the second phalanx,—is a point

[1] I had not done this when my account of *Stagonolepis* was given to the Society, and hence, in the abstract of my communication, the comma-shaped impression is described as the mark of a "thick, short, and much-curved nail."

I will not take upon myself to decide. A concave surface, rising anteriorly, connects the impression of the proximal moiety of the first digit with that of the proximal phalanges of the second digit. This impression, which is about an inch long, is very deep, especially at its posterior end, and consists of two divisions, joining at an angle, which is open outwards. The posterior division is shorter and broader than the anterior, and the two would answer very well to two phalanges; the anterior division is succeeded by a third elongated and much fainter impression, about $1\frac{1}{4}$ inch long, broad and tolerably deep at the base, but gradually tapering and fading away anteriorly. This appears to be the impression of the ungual phalanx of the digit; so that it would appear that there were three phalanges in this digit, that the direction of the proximal one is straight forwards, that of the middle phalanx forwards and outwards, and that of the distal or ungual phalanx still more outwards; so that the three describe a kind of curve, convex inwards.

The impression of the third digit is like that of the second, except that the distance between what appears to be the end of the proximal phalanx and the base of the ungual phalanx (corresponding with the 'anterior division,' spoken of above) amounts to fully $\frac{3}{4}$ inch, while in the second toe it is not more than $\frac{1}{2}$ inch. Perhaps there were two phalanges here. The impression of the ungual phalanx is, as was stated above, $1\frac{1}{4}$ inch long.

The impression of the fourth toe is shorter than that of the third; but, as the ungual phalanx is of nearly the same length as in the third, the shortening would appear to be due either to the shortening, or to the smaller number, of the proximal phalanges.

The impression of the fifth digit does not quite reach to the base of the ungual phalanx of the fourth. The impression of the terminal phalanx is less distinct, and, like the fourth, the stirring up of the sand has rendered it indistinct at its proximal end.

The surfaces of the interspaces between the digits are so peculiarly rounded that there can be little doubt they were moulded by a connecting membrane or web, though the precise boundaries of this interdigital membrane are not traceable.

(*Hind Foot.*)—The ends of the toes of the posterior impression of the pair to which that just described belongs infringe upon the posterior and outer part of the plantar margin of the anterior impression. It is but a confused mark, however, and the true characters of the imprint left by the hind foot are much better shown in the pair behind these, where the sand was evidently firmer when the animal walked over the surface.

This impression (fig. 5) measures about $2\frac{1}{4}$ inches transversely, and longitudinally $2\frac{1}{2}$ inches, or a little less.

The planter surface measures $1\frac{1}{8}$ inch from before backwards, and its posterior edge is nearly semicircular and not emarginated. The anterior edge is nearly straight. It gives off four deepish longitudinal impressions, answering to as many digits. Of these the middle two measure $1\frac{1}{8}$ inch in length, and are consequently somewhat longer than the inner and the outer, which are hardly more than $\frac{3}{4}$ inch long.

The ungual phalanges appear not to have attained a length of $\frac{3}{8}$ths of an inch in the longest digits, and all four digits appear to have been connected by a web. The anterior and external angle of the plantar surface projects $\frac{3}{8}$ths of an inch beyond the base of the fourth digit, as if there had been a rudimentary fifth digit.

The length of the stride, from the hinder edge of one fore-foot print to that of the next, is just twelve inches. The space covered by the track transversely to its length, measured from the outer edge of one footmark to a line prolonging that of the footmark on the opposite side, is about ten inches.

On the same slab as that on which these tracks occur there are a number of other footmarks, some of which are nearly eight inches long, while others hardly exceed an inch in length. They are all, however, more or less imperfect, either from the condition of the surface at the time they were impressed, or from the subsequent superposition of other impressions. The only feature which they exhibit better than those just described is the mark of the interdigital membrane, which in some of these footmarks is very obvious, and exhibits strong transverse wrinkles, concave forwards.

All the other foottracks from Cummingstone which have come under my notice are either mere unintelligible marks, or may be explained by the perfect footsteps I have just described; so that at present I see no reason for believing that the tracks were caused by more than one species of Reptile. The great apparent differences between some of these footmarks and others appear to be referable to the varying condition of the sand upon which the tracks were made.

In the length of the impressions made by the ungual phalanges, and in the large size of the anterior as compared with the posterior foot, the Cummingstone tracks are, so far as I know, unlike those of any known Crocodilian or Chelonian (?) reptile; but it must be confessed that there is a great want of recent materials in attempting to study comparative ichnology. The footmarks in question are not

Cheirotherian, nor do they present any marked similarity to the singular tracks found at Shrewley Common. The resemblance to some of the Ichnites (*Chelichnus*, *e.g.*) of Dumfriesshire, though closer, by no means amounts to identity. But I defer for the present a more extended comparison, which could only be made intelligible by numerous figures.

As to the question whether these tracks were or were not produced by *Stagonolepis*, I will only say that I see no reason for asserting that they were not, while there is some ground for believing that they were so produced. There is reason to believe that *Stagonolepis* had a short and broad metatarsal and metacarpal region and long ungual phalanges. The footprints have broad palmar and plantar impressions and long claw-marks. The shape of the claw-mark answers very well to that of the sole ungual phalanx which has been discovered; but I must remark that the length of that phalanx is somewhat too great for any footprint yet discovered.

The Crocodilian number of toes, again, combined with the non-Crocodilian proportions of the feet, harmonizes very well with the modified Crocodilism (if I may coin a word) of the organization of *Stagonolepis*.

NOTE.—Unless the contrary is expressly stated, the preceding paper remains in all essential respects the same as when it was sent in to the Society. Since that time, however, several months have elapsed, and, thanks to the exertions of my indefatigable friend Mr. Gordon, much new material has come to light. On the other hand, I have submitted the recent *Crocodilia* to such a revision as the time at my disposal would allow, and I have published some of my results in an Essay "On the dermal armour of *Jacare* and *Caiman*, with notes on the specific and generic characters of recent *Crocodilia*," published in the 'Proceedings of the Linnean Society' for February, 1859.

The sum of my conclusions from the various kinds of evidence thus obtained is, that the divergence of *Stagonolepis* from the Crocodilian type is even less than I had imagined; and in some characters, such as the form of the posterior maxillary teeth, *Stagonolepis* is more like a modern Crocodile than a Teleosaurian.

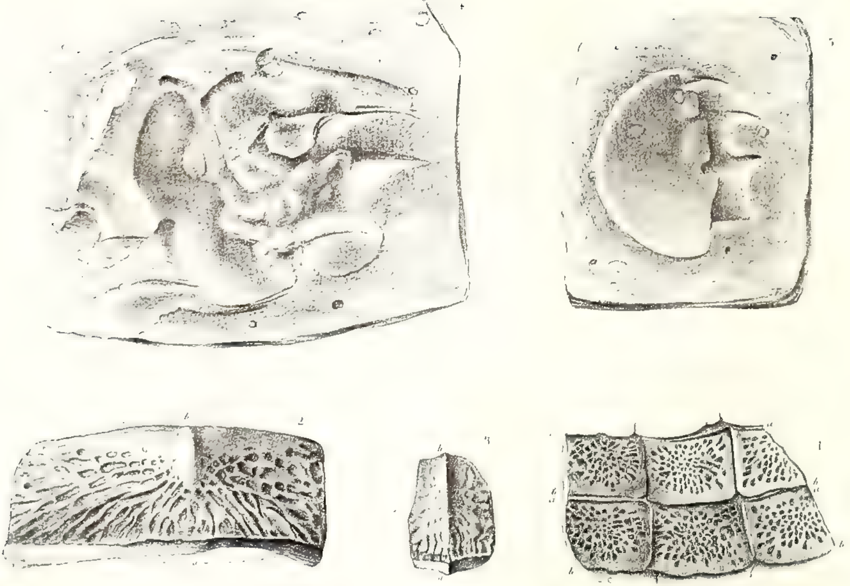
A very fine specimen of a coracoid, recently sent by Mr. Gordon, convinces me that the differences from the Crocodilian type of structure which I have ascribed to this bone in *Stagonolepis* do not really

exist. I am obliged to take this opportunity of distinctly asserting that the only two coracoids of *Stagonolepis* which have been discovered have been sent to me direct from Elgin, that I have worked them out from the matrix with my own hands, and that no anatomist had seen the one described in my paper before the publication of my account of its structure. That account, however, is incomplete, the new specimen showing that a considerable part of the bone was wanting, and that, when perfect, it is far more Crocodilian than Lacertilian in its characters.

The remarkable new Reptile, *Hyperodapedon Gordoni*, which I have briefly characterized in a note to Sir R. I. Murchison's paper (see p. 435), is of paramount interest; for while, on the one hand its discovery justifies my hesitation in at once ascribing the Cummingstone footmarks to *Stagonolepis*,—on the other, its marked affinity with certain Triassic reptiles, when taken together with the resemblance of *Stagonolepis* to mesozoic *Crocodilia*, leads one to require the strongest stratigraphical proof before admitting the palæozoic age of the beds in which it occurs.

Finally, I may add, that *Stagonolepis* attained a much greater size than my former materials warranted me in believing. Some of the recent discoveries lead me to suppose that it reached 16 or 18 feet in length.

While this Note was passing through the press, the Monograph of D'Alton and Burmeister ('Der fossile Gavial von Boll,' 1854) came into my hands. The excellent memoir by these authors on the ancient *Mystriosaurus bollensis* is preceded by a valuable essay on the organization of recent *Crocodilia*, including the best account I have met with of the ventral dermal armour (p. 29). The transverse sutures dividing the ventral scutes, and their mode of articulation, are noted; but, on the other hand, it is said that only the three or four outer series of ventral scutes have pitted surfaces, and the authors suppose that the ventral armour which they describe (and which is apparently that of a *Jacare*) is found in all recent Crocodiles. I can find no reference to the fact that the great majority of living *Crocodilia* are wholly devoid not only of ventral bony armour, but of *articulated* dorsal scutes.—July 5, 1859. T. H. H.



STAGONOLEPIS.

DESCRIPTION OF PLATE XIV. [PLATE 6.]

Fig. 1. Plaster-cast of a portion of the specimen of *Stagonolepis* originally described by Professor Agassiz. *a*, anterior ends of the *flat scutes*; *b*, their posterior ends.

Fig. 2. Gutta-percha cast of the impression of a *broad-angulated scute* (not that described in the text), from Findrassie.

Fig. 3. Gutta-percha cast of an impression of an *irregular-angulated scute*, from the same locality.

Fig. 4. Right anterior footprint, from Cummingstone.

Fig. 5. Right posterior footprints, from the same series of tracks.

VI

ON SOME AMPHIBIAN AND REPTILIAN REMAINS FROM SOUTH AFRICA AND AUSTRALIA

Quarterly Journal of the Geological Society, vol. xv., 1859, *pp.* 642-649.
(*Read March 23rd*, 1859.)

PLATES XXI., XXII. [PLATES 7, 8.]

AT the Evening Meeting of this Society, held on the 17th of November, 1858, a paper by Mr. Stow "On some Fossils from South Africa" was read. In the course of the discussion which followed, my opinion as to the nature of one of those fossils was asked. With so much reserve as was due to the cursory character of my examination of the remains, I expressed my conviction that the organism in question was the skull of a Labyrinthodont Amphibian, and briefly stated the grounds upon which I based that conclusion. The Chairman of the Meeting then called upon me to undertake a thorough investigation of the matter; and I now report the results of my inquiries in the first of the following papers, in which I have embodied, incidentally, the description of an allied Australian Amphibian.

1. *On* Micropholis Stowii *and* Bothriceps Australis.

Micropholis Stowii.—The skull in question is $1\frac{5}{8}$ inch long, and has, when viewed from above, a parabol icoutline (Pl. XXI. [Plate 7] fig. 1), or it might be compared to the half of a long ellipse, half of the longer diameter of which is to its shorter diameter as 13 to 10. The bony plates which formed the roof of the skull (fig. 1) have entirely disappeared, as have those which constituted the greater part of its right lateral parietes; but on the left side (fig. 2), the lateral walls are in a tolerably good state of preservation.

The matrix has split in such a manner that that portion of it

which is bounded by the contour of the skull has separated from the rest, leaving in its concave counterpart the outer bony crust of the mandible and a portion of the maxillary bones. I had hoped that the fossil might be relieved in such a manner as to show, not only the structure of the under part of the skull, but the character of the occipital articulation; but the matrix is so exceedingly hard, and the bony matter so soft and fragile, that even my experienced and skilful ally, Mr. Dew, was afraid of carrying on his excavations sufficiently far to attain these objects.

Sufficient has been done, however, to reveal the indistinct remainder of the anterior part of the vertebral column, and to prove, by its means, at what point the occipital region of the skull was situated. From this it appears that the postero-lateral angles of the cranium were produced for $\frac{3}{8}$ths of an inch behind the general plane of the occipital surface.

The most striking features in the skull are the large oval orbits, which occupy, as nearly as may be, the middle third of the space between the occiput and the end of the snout. The long axes converge a little anteriorly; and the interorbital space (which is not equal to more than one-fourth of the diameter of the skull), opposite the middle of the orbits, is far narrower than the transverse diameter of the orbit.

The nostrils are rounded apertures, distant less than twice their own antero-posterior diameter from the anterior edge of the orbit; they are placed very near the anterior edges of the snout, and are separated transversely by an interval equal to the interorbital space. Their long axes are, like those of the orbits, directed obliquely inwards and forwards. Both orbits and nostrils look upwards and outwards, the former direction predominating. The vertical diameter of the skull (including the mandible) is greatest posteriorly; but even here the thickness does not attain one-fourth of the length; and the vertical diameter gradually diminishes anteriorly, until, at the end of the snout, the thickness does not exceed an eighteenth of the length.

The left premaxillary bone appears to be nearly entire. It is very short, its horizontal portion extending backwards only to the middle of the external nostril, the anterior part of whose inferior boundary it forms. At its inner end, the premaxilla gives off a broad but short, ascending, recurved process, which forms the anterior and internal boundary of the external nostril and ends superiorly in a point. Whether it is broken off here, or not, I cannot say.

The maxilla meets the posterior end of the premaxilla, and then

extends backwards beneath the orbit to the posterior margin of the jugal bone, where its bony matter disappears. The maxilla is widest midway between the nostril and orbit, where it sends up a short obtuse process.

Immediately above this portion of the maxilla lies a broad flat bone (Pl. XXI. [Plate 7] fig. 2), circumscribed on three sides by a zigzag suture, whose posterior free edge forms the anterior boundary of the orbit, while its anterior margin does not quite reach the posterior boundary of the external nostril. Its upper edge unites with a fragment of bone whose anterior end enters into the boundary of the nostril. Inferiorly and behind, it is in contact, for a small extent, with a bone (the jugal) which completes the boundary of the orbit below; and, in front of this point, it either comes into relation with the maxilla, or is separated from it by an elongated bone which completes the boundary of the nostril anteriorly. I put the alternative because I do not feel certain whether a particular line, which seems to be a suture, is one or not. If the elongated strip of osseous matter in question be a distinct bone, it corresponds with that termed by Von Meyer "lacrymal" in the Labyrinthodonts.

The bone bounded by the zigzag suture is in all probability the prefrontal, while the upper fragment connected with it is apparently all that remains of the nasal.

The jugal bone (Pl. XXI. [Plate 7] fig. 2) narrows as it passes back from its connexion with the prefrontal, becoming very slender where it forms the lowest part of the orbital wall. Indeed it here exhibits a discontinuity; but I believe this to be the result of fracture. At the posterior part of the orbit it expands into a broad plate, whose anterior concave margin forms half of the posterior boundary of that cavity. Its inferior margin unites with the maxillary, and then with a small triangular plate of bone interposed between it and the end of the maxillary (quadrato-jugal?). Its superior margin is divided into two parts,—an anterior, nearly horizontal, which unites with a slender plate of bone whose anterior end forms part of the boundary of the orbit, and seems to be all that is left of the bone called "post-orbital" (Hinteraugenhöhlen-knochen) by Von Meyer; and a posterior moiety, which shelves downwards and backwards and articulates with another fragmentary bony plate, whose upper part occupies the superior and external angle of the skull, while its lower part becomes lost in the outer surface of the mass of matrix which has filled the cavity formed by the quadrate and other bones, and is the representative of the suspensorial apparatus of the lower jaw. This bone is obviously the squamosal.

On the left side, the bones which should constitute the lower end of the mandibular suspensorium have almost entirely disappeared, a small fragment only of the quadratum remaining. On the right side, however, a considerable proportion of the quadratum is preserved (Pl. XXI. [Plate 7] fig. 4). Its articular end, $\frac{3}{16}$ths of an inch broad, and flattened from above downwards, exhibits a condyloid surface which is divided by a groove into a stronger internal, and a less prominent external portion. In front of the condyles the quadratum is very thin, but it rapidly expands, so as to cover all that remains of the flat lateral face of the suspensorium, and extends forward to about midway between the articular condyle for the mandible and the posterior margin of the orbit. At this point the bony matter disappears. On the top of the skull all the osseous matter has vanished except two white lines, one on each side of the interorbital space (representing the upper edges of the orbito-sphenoids?), and a sinuous transverse line faintly indicating the contour of the occiput (Pl. XXI. [Plate 7] fig. 1).

The lower jaw (figs. 2, 4, 5) has the same general outline as the anterior and lateral contours of the skull. Its rami are slender in front, but deep and strong posteriorly, where there is a faint indication of a coronoid elevation, in correspondence with which the inferior margin of the suspensorial peduncle is slightly excavated. Behind this the ramus rapidly narrows to its posterior extremity, which extends very little beyond that of the quadrate bone. At the symphysis, the dentary element of the mandible is very distinct and is rather less than $\frac{1}{8}$th of an inch in width; it extends back, becoming more slender as it goes, along the upper edge of the mandible. Its posterior boundary cannot be exactly traced; but the backward continuation of the series of teeth with which it is beset testifies to its elongation beyond the level of the posterior margin of the orbit. The symphysial end of each dentary bone is concave and produced into a short process posteriorly, so that the union of the two rami would seem to have been somewhat lax (fig. 3).

The counterpart of the fossil (figs. 1, 2, 3) just described exhibits the dentary bone of the right ramus in transverse section. It is triangular, with a thin internal edge and a flat upper surface. The teeth are set in apparently distinct alveoli along its outer moiety; and beneath them runs a canal filled with matrix.

A second osseous element of the mandible, the angular bone, extends on the inner side of the jaw to within $\frac{3}{16}$ths of an inch of the symphysis. It is trough-like (fig. 5), consisting of an internal and an external lamella, united at an angle below, and it appears to

extend back nearly to the posterior extremity of the ramus. The precise boundaries of the third distinguishable component of the mandible, the articular bone, are not to be made out; but on the left side, the matrix which fills the posterior end of the ramus extends forwards, becoming narrower until it ends by a slender rounded extremity, coated with a bony sheath, between the angular and the dentary, and near the anterior termination of the latter. On the right side, in the counterpart, the section of this style-like process of the matrix is seen, and seems to be connected with a narrow bony plate, which appears on the inner side of the ramus between the dentary and the angular.

The posterior end of the articular element is broad and somewhat produced internally, so as to afford sufficient space for the adjustment of the wide articular end of the suspensorial peduncle.

On the under surface of the skull (fig. 3), a whitish patch may be observed on the inner side of the anterior part of the right ramus of the mandible, and a much larger transverse band, of a similar aspect, stretches from the posterior part of the left ramus, two-thirds of the way across to the opposite one.

When these patches are minutely examined, they are seen to consist of a multitude of small, flat, polygonal scutes, of very various dimensions and forms, but none exceeding $\frac{1}{16}$th of an inch in diameter. These minute scutes are fitted together by their edges; and their surfaces are marked by irregular grooves and pits, which are so disposed as to leave a narrow, clear margin (fig. 7).

Between the posterior extremities of the rami, the same surface of the fossil exhibits on each side the indistinct impression, and part of the bony substance, of a broad, flat, triangular plate, whose base is turned inwards, and whose apex is produced and bent upwards. Two other fragmentary bones, of apparently a similar character, lie behind these; and still further back, on the counterpart, are the remains of what I take to be a portion of the pectoral arch and its appended member; but the parts are so indistinct and fragmentary that it would be vain to describe them particularly.

The teeth (fig. 6) are very numerous and close-set, slender, conical, sharply pointed, and either straight or concave inwards. They are stronger in the lower jaw than in the upper, and in the anterior than in the posterior part of the lower jaw. I could observe no distinct traces of those longitudinal grooves which characterize the teeth of the larger Labyrinthodonts; but they seem to have possessed a large pulp-cavity. While the teeth of the mandible appear (as I have said) to be lodged in distinct though shallow alveoli, those of the

upper jaw seem to be completely anchylosed with the bony walls of the jaw, so as to look like mere processes of it. I would be understood to speak with considerable hesitation on these points, however, the parts being but very imperfectly preserved.

It is at once obvious that the skull which I have just described could have belonged to no true Reptile, but is either that of an Amphibian or that of a Fish.

The composition of the lower jaw, the characters of the teeth, the well-developed nasal apertures, and the arrangement of the bones in the temporal region leave no doubt in my mind as to which of the latter alternatives is to be preferred, and satisfactorily prove the amphibian affinities of the fossil.

Such being the case, there is but one order of the *Amphibia*, as they are at present arranged, to which it can be referred—the *Labyrinthodonta*,—with a knowledge of whose characteristic peculiarities, so much of the structure of the skull as can be made out becomes readily intelligible. Thus, in shape and in the position of its orbital and nasal apertures, the African fossil presents a certain resemblance to the German Labyrinthodont *Metopias*, and to the imperfectly known Russian *Rhinosaurus*. The arrangement of the cranial and facial bones, and their ornamentation, coincide very well, so far as they go, with the corresponding features of those Labyrinthodonts which have been best studied; and the peculiarities of the jugal, postorbital, and squamosal bones are especially characteristic. Again, I should hardly have ventured to interpret so confidently the appearances presented by the mandible, had I not recently had an opportunity of studying the composition of its articular moiety in some portions of very large mandibles of *Labyrinthodon*, or *Mastodonsaurus*, from Warwickshire. I find, from these fossils, that the articular element of the Labyrinthodont jaw (in these genera at any rate) sends a hollow bony prolongation (at first probably a mere osseous sheath around Meckel's cartilage) for a long distance towards the symphysial end of the jaw; and I suspect that the cone of matrix which I have described above is nothing but the cast of a similar prolongation. In the Warwickshire Labyrinthodont, a strong process, formed partly by the angular and partly by the articular bone, is given off inwards and forwards from the posterior part of the inner surface of the ramus; and this is perhaps represented by the inward production of the posterior part of the ramus of the mandible in the African fossil. On the other hand, the great Labyrinthodonts have a very distinct angular process prolonged backwards behind the articulare, and composed in great measure of a process of that

element, as in the Crocodile—a structure of which I see no trace in the fossil under consideration.[1]

The large bony plates under the throat suggest a comparison with the similarly proportioned bony plates which occupy a like position in so many of the better-known Labyrinthodonts, such as *Mastodonsaurus*, *Archegosaurus*, &c. Of these plates, however, there are only three, a median (rhomboidal), and two antero-lateral (triangular and bent up at the sides); while the present fossil seems to exhibit the remains of four plates, in two pairs, all of which have the form of triangles with their bases inwards. I am inclined to think that these parts are, in fact, the remains of a hyoidean system, possibly indicating a long persistence of the branchial apparatus.

The teeth, in their even size, their very large pulp-cavities, and the apparent absence of folds of their dentine, are not much like those of the typical Labyrinthodonts; but it must not be forgotten that our own Red Sandstone series[2] contain a Labyrinthodont (the so-called *Labyrinthodon Bucklandi*) which is a totally distinct generic form[3] from any of the described Labyrinthodonts, and has close-set, conical, thin-walled teeth, so anchylosed with the upper jaw as to appear continuous with it.

But the Labyrinthodont remains to which the African skull presents the closest resemblance are the *Brachyops laticeps* of Central India, and the undescribed cranium of an animal (from Australia) in the British Museum, very closely allied to *Brachyops*.

Brachyops laticeps has been already so fully described by Professor Owen,[4] that I need merely refer to his paper and to the figures accompanying it: by studying these any person may convince himself of the general resemblance between the Indian and the African fossil, and, at the same time, of the clear differences which separate them generically.

The precise locality whence the Australian skull was obtained is unknown; and I should have remained ignorant of its existence except for the kindness of my friends Mr. Waterhouse and Mr.

[1] Since this paper was read, I have published an account of the structure of the Labyrinthodont jaw to which reference is made, in Mr. Howell's "Memoir on the Warwickshire Coal-field": Memoirs of the Geological Survey, 1859.

[2] I learn from Professor Ramsay that the stratum in which *Dasyceps Bucklandi* occurs is of Permian, not of Triassic age.

[3] I therefore propose to change its name into *Dasyceps Bucklandi*, the generic appellation alluding to the singularly rough and prickly surface of the cranial bones, like that of some recent *Bratrachia*. (See Mr. Howell's Memoir cited above, in which the cranium of *Dasyceps* is described and figured.)

[4] Quart. Journ. Geol. Soc., vol. x. p. 473; and vol. xi. p. 37.

Woodward, the latter of whom, being present when I gave a short description of the African fossil to the Society, was struck with its resemblance to the skull in the British Museum.

Bothriceps Australis.—In the Australian fossil (Pl. XXII. [Plate 8] fig. 1) the bony matter has almost wholly disappeared from the roof of the skull, except near the occiput, where a patch of it remains in the supraoccipital region, and is sculptured like the corresponding part of a Crocodile's skull, exhibiting irregular close-set, but separate, polygonal pits. The cranium measures four inches in length, from the extremity of the snout to the end of the occipital condyles, and its greatest breadth between the ends of the mandibular suspensoria is $3\frac{3}{4}$ inches; the greatest depth of the skull is at its posterior end, and does not exceed $1\frac{1}{2}$ inch, so that it is very flat (fig. 2). The margins of the left orbit are much broken; but those of the right orbit seem to be nearly entire. It is oval, with its long axis directed forwards, nearly parallel with that of the skull; it measures $\frac{7}{8}$ths of an inch in breadth, $\frac{5}{8}$ths of an inch in width, and it occupies as nearly as possible the middle of the space between the superior margin of the occiput and the anterior edge of the premaxilla. The interorbital space appears to have measured about an inch in width. The posterior margins of the large rounded nasal apertures are distant about $\frac{3}{4}$ths of an inch from the anterior margin of the orbits; and the interspace between the nostrils is about half an inch.

The surface of the matrix exhibits impressions of the sutures which separated the constituent bones of the skull. Two nasals, two large frontals, and a single or double parietal are clearly traceable in the middle line. The middle of the anterior half of the parietal region is marked by a strong longitudinal depression, which occupies nearly one-third of its width, and ends, posteriorly, in the parietal foramen, while anteriorly it is continued forwards, becoming shallower, on to the frontals. The postfrontal bounds most of the inner and a little of the posterior margin of the orbit, while almost the whole of the remaining posterior boundary is filled up by the postorbital bone. Posteriorly and externally, this joins the squamosal; while posteriorly and internally, a bent sutural line separates it from a bone which is called "squamosum" by Von Meyer, *Archegosaurus*, and "second parietal" by Professor Owen in *Brachyops*. This bone and the squamosal unite posteriorly with a pyramidal bone which resembles in form and position the bone called "occipital externe" in Fishes by Cuvier. The exoccipitals project for half an inch below the occipital foramen, to form the two stout occipital condyles, which have unfortunately been sawn through.

I can find no indication of a suture in the bony plate which covers the supraoccipital region. The quadratum is cut away on one side, and so embedded in the matrix, on the other, that its form cannot be made out. The whole suspensorium, however, projects downwards and backwards. The lower jaw has the same parabolic outline as the skull; but some adherent matrix must be cleared away before its exact proportions and constituents can be made out. The teeth are very numerous, and close-set, not more than $\frac{1}{8}$th of an inch long. They are conical, straight, and sharp-pointed; and their bases are expanded, and marked by about twelve longitudinal folds, which extend to near the apex of the tooth.

On comparing this fossil with *Brachyops laticeps*, its proportions are seen to be widely different, though the two skulls have within half an inch of the same length; and therefore specific identity is out of the question. Indeed, considering the additional difference in the relative size, in the form, the position, and the direction of the orbits, I conceive that the Australian fossil may be safely regarded as the type of a new genus, for which I propose the name of *Bothriceps*, in allusion to the peculiarly pitted character of the sculpture of such of the cranial bones as are left. I should, indeed, have been disposed to bring forward this pitted sculpture more prominently in alluding to the difference between this genus and *Brachyops*, were it not that the character of the surface of that part of the skull of the latter fossil which corresponds with all that is left of the cranial bones of *Bothriceps* is not clearly discernible. The present species may be called *Bothriceps Australis*.

Whatever be the relations between the Australian and Indian fossils, the evidence, as it stands at present, justifies our regarding both as generically distinct from the African Labyrinthodont, whose dermal scutes alone separate it from all other members of the group, the scutes of *Archegosaurus* having perfectly different characters.[1]

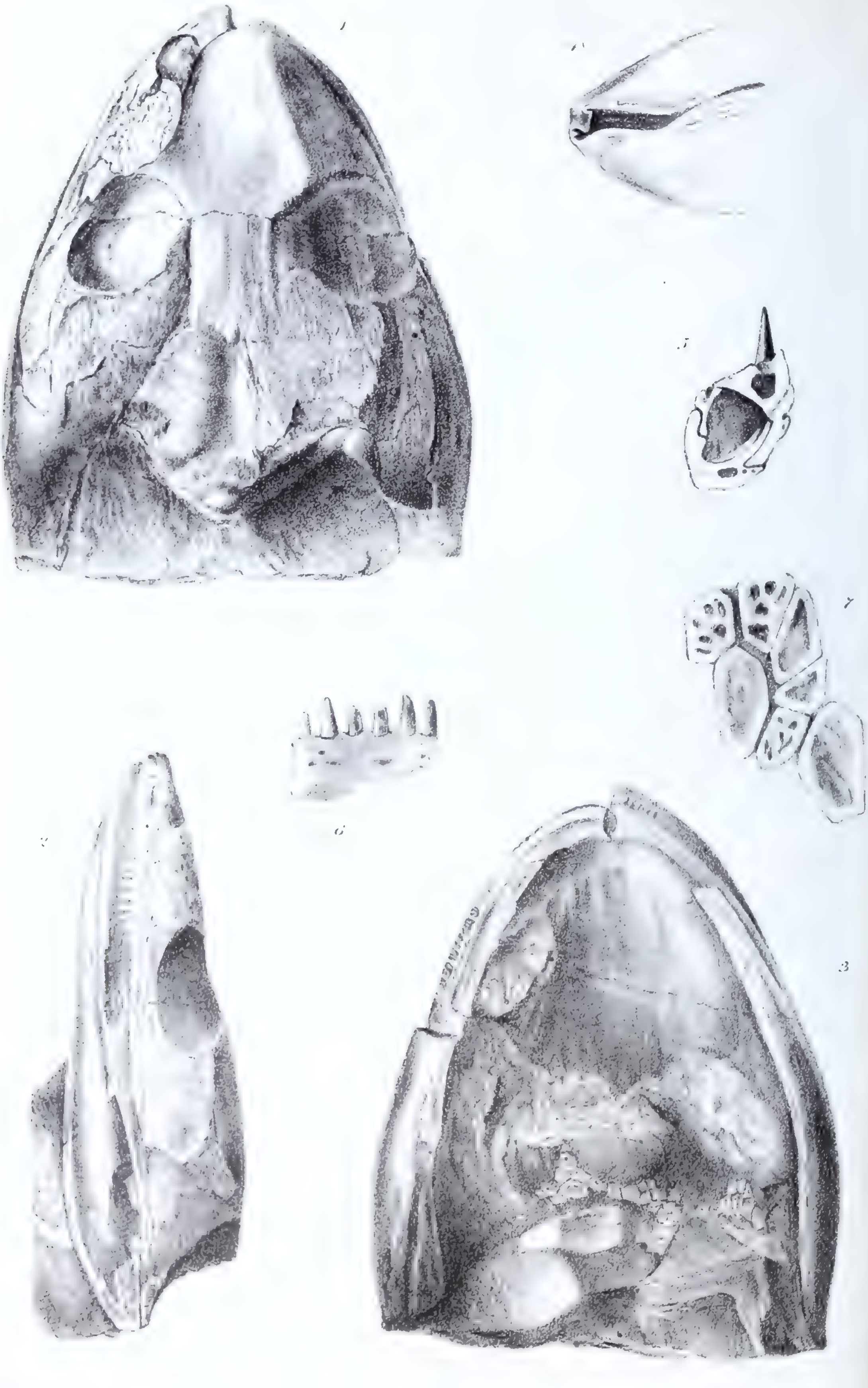
I propose therefore to form a new genus, *Micropholis*, for this African fossil, and to call it *Micropholis Stowii*, after its discoverer,[2] who has the merit not only of finding the fossil, but recognizing its Batrachian affinities, sending home with it the skull of that African Frog which seemed to him most nearly to approach it.

The concurrence of Labyrinthodont remains with the beaked and

[1] There is no certainty that the *Anisopus scutulatus* (Owen) of the Warwickshire Trias is really a Labyrinthodont; and if it proves to be such, its scutes are very different from those of *Micropholis*.

[2] Quart. Journ. Geol. Soc., vol. xv. p. 193.

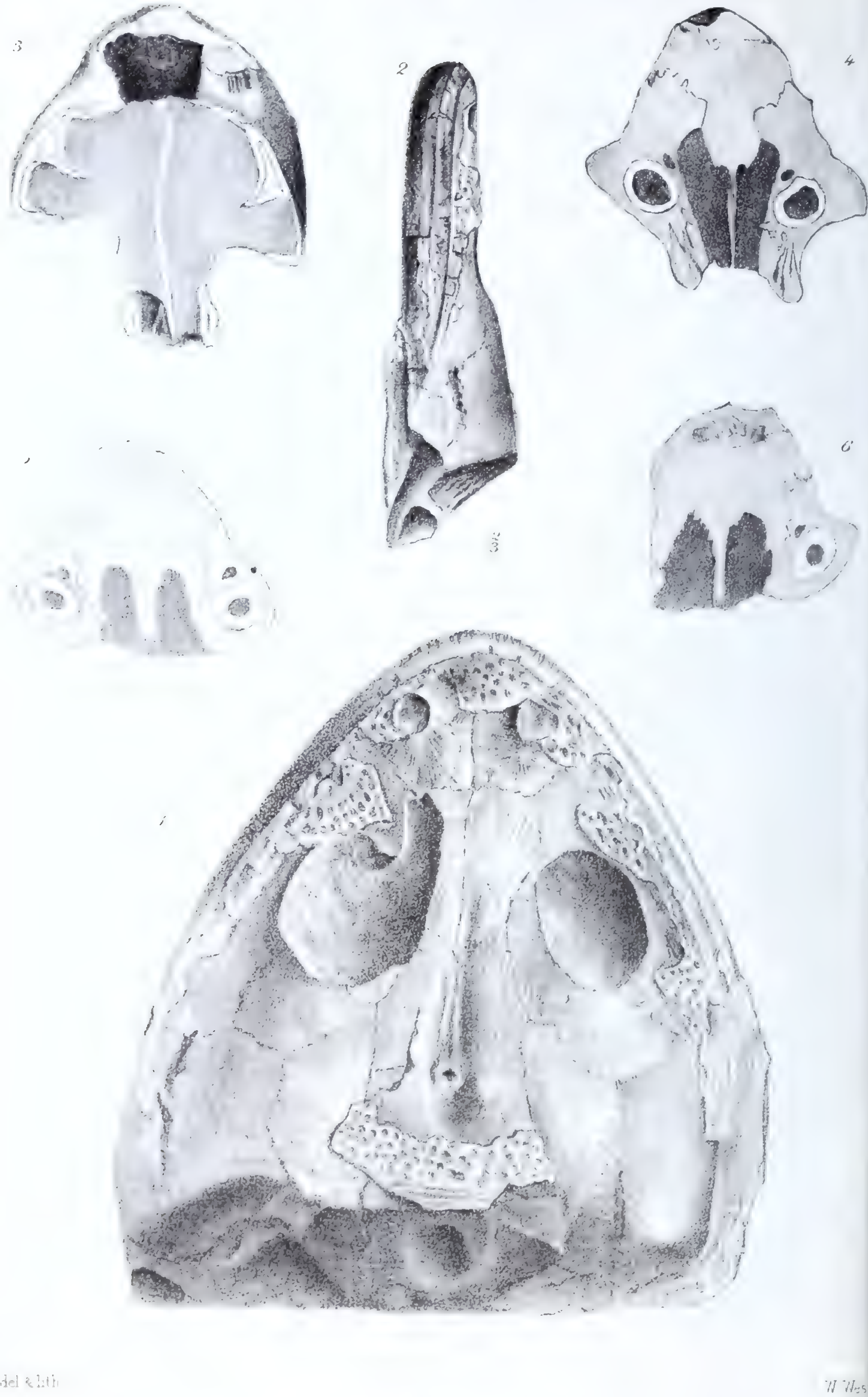
[PLATE 7]



W West imp

STOWII

[PLATE 8.]



G West del & lith

W West im

[illegible] AUSTRALIS & DICYNODON MURRAYI

few-toothed or toothless Dicynodont Reptiles[1] in the Karoo-beds of Africa presents so striking a resemblance with the assemblage of Reptiles characteristic of the Fauna of the Trias in this country, that one is at first inclined to leap to the conclusion, that the discovery of this association settles the question of the age of the African formation. When I consider, however, that Labyrinthodont *Amphibia* range from the Lias down to the Carboniferous formations inclusive, and that *Micropholis* is not very closely allied to any of the more characteristic forms of the Trias, I am inclined to pause before drawing any very decided inference from the analogy of the Faunas.

[1] Mr. Stow collected in the same locality (at the foot of the Rhenosterberg), together with the *Micropholis*, some Dicynodont remains, to which I hope to return on a future occasion.

DESCRIPTION OF PLATES XXI. AND XXII. [Plates 7, 8].

Plate XXI. [Plate 7].

Fig. 1. Skull of *Micropholis Stowii*, viewed from above. Magnified 2 diameters.
Fig. 2. The same, seen from the left side. Magnified 2 diameters.
Fig. 3. The same, seen from below. Magnified 2 diameters.
Fig. 4. The posterior end of the right ramus of the mandible, and of the mandibular suspensorium of the same.
Fig. 5. Transverse section of the mandibular ramus.
Fig. 6. A portion of the mandible, with teeth *in situ*.
Fig. 7. The dermal scutes represented in fig. 3, magnified 10 times.

Plate XXII. [Plate 8].

Fig. 1. Dorsal or superior view of the cranium of *Bothriceps Australis*. Nat. size.
Fig. 2. Lateral view of the same, reduced to one-third diam.
Fig. 3. Transverse section of the snout of *Dicynodon Murrayi*, taken perpendicularly to its axis, just in front of the internal nares. Reduced to one-half diam.
Figs. 4, 5, 6. Similar sections, taken successively nearer the extremity of the snout. Reduced to one-half diam.

VII

ON A NEW SPECIES OF DICYNODON (*D. MURRAYI*), FROM NEAR COLESBERG, SOUTH AFRICA; AND ON THE STRUCTURE OF THE SKULL IN THE DICYNODONTS

Quarterly Journal of the Geological Society, vol. xv., 1859, *pp.* 649–658.
(*Read March 23rd*, 1859.)

PLATE XXIII. [PLATE 9].

IN the spring of 1858 the Rev. H. M. White of Andover brought to the Museum of Practical Geology some fossils from South Africa, with whose nature he desired to be acquainted. Among them was a fragment of the skull of a *Dicynodon*, which, on comparison with the species already described, appeared to me to be new. On applying to Mr. White for further information about the fossil, that gentleman was good enough to put me in communication with its discoverer, Mr. J. A. Murray, who, on learning what interest attached to the skull, very kindly undertook to procure a supply of more perfect remains of the same Reptile from his father, who resides near Colesberg in South Africa, and not very far from the junction of the Orange and Caledon Rivers, where the fossil was found. Under these circumstances I thought it better to abstain from publishing the new species until the promised additional materials should have come to hand. They arrived at the end of the year; and in January, 1859, Mr. Dew, of the British Museum, to whom I had entrusted the working out of one of the three (nearly entire) crania which Mr. Murray had sent, brought me the skull figured in Pl. XXIII. [Plate 9], which, I had the satisfaction to find, fully bore out the view I had taken of the specific distinctness of the fragment

which first came into my possession. I had then no hesitation in desiring to lay my results before this Society; and on the 2nd of February the President assigned me the evening of the 23rd of March for this and certain other communications.

In the meanwhile, the Society happening to be but scantily supplied with papers on the evening of the 23rd of February, I exhibited the cranium of my new *Dicynodon*, defined its characters, and conferred upon it the name of *D. Murrayi*, after the gentleman to whose exertions I was indebted for my materials.

The cranium of *Dicynodon Murrayi* (Pl. XXIII. [Plate 9] fig. 1) measures seven inches in a straight line from the extremity of the occipital condyle to the extremity of the snout, and six inches along a line drawn from the highest point of the roof of the skull to the articular extremity of the quadrate bone. From the extreme outer point of the left quadrate bone (the right is somewhat damaged) to the centre of the occipital condyle is a distance of four inches; so that the back of the skull is eight inches wide. The highest point, or vertex, of the skull lies a little in front of the posterior boundary of the orbit, and is situated, as nearly as may be, opposite the middle of the horizontal axis of the skull. The occipital condyle is a little broken at its extremity, but still projects half an inch beyond the plane of the occipital foramen.

The posterior part of the superior region of the skull, or that which lies between the temporal fossæ, looks backwards as well as upwards, so as to form an angle of about 30° with a line joining the snout and the occipital condyle. Between the orbits the contour of the cranial roof is rounded from before backwards, and so passes into the preorbital region, which slopes abruptly downwards and forwards, so as to form an angle of 90°—100° with the plane of the intertemporal region. As both the anterior and the posterior ends of the head are obliquely truncated, its entire lateral contour appears like a pentagon, whose apex, formed by the vertex, is directed upwards, and its base, formed by the mandibles, is turned downwards. On the other hand, viewed from in front or behind (Pl. XXIII. [Plate 9] fig. 2), the skull has rather the form of a hexagon, whose superior side is constituted by the interorbital space, its supero-lateral sides by the edges of the postfrontal bones, its infero-lateral sides by the quadrate bones, and its base by the interval between the rami of the mandibles. The superior face of the skull is narrower in front than behind, where it presents a deep and wide median excavation, formed by the divergence of two strong processes, which expand at their ends and unite with a straight, strong, bony bar,

which lies parallel with the longitudinal axis of the skull, and consequently nearly at right angles with them. Anteriorly this bony bar becomes connected with the process which forms the posterior boundary of the orbit. The upper wall of the cranium itself is very narrow, measuring only 1·3 inch across posteriorly, but it expands anteriorly, until, at the level of the posterior margins of the postorbital processes, into which its margins gradually pass, it is 2 inches wide.

The supratemporal fossæ, circumscribed by these parts on each side, are 3 inches wide by 1½ inch long; and while their anterior, posterior, and external boundaries are nearly straight, the inner boundary, formed by the walls of the cranium proper, is concave. The narrow and flattened intertemporal region of the skull expands anteriorly into the interorbital region, which has a nearly square outline, 3½ inches wide by 3 inches long. It is convex from before backwards, and exhibits a slight median ridge, which is much more marked in the original fragmentary specimen than in that figured.

I have not been able to detect any clear evidence of the existence of a parietal foramen in this skull; but in another specimen it is situated in the middle of a line drawn from the anterior margin of one temporal fossa to that of the other.

Anteriorly the interorbital space is bounded by two strong converging ridges (less distinct in this specimen than in others), which pass forwards and inwards, to meet in the middle, rather behind a line uniting the anterior and inferior margins of the orbits. Here they are joined by the low longitudinal ridge which has been stated to traverse the interorbital region.

Each of the converging ridges exhibits a thickening rather internal to its middle, which is continued for a short distance obliquely inwards.

In front of the orbits the facial bones form a thick mass, produced downwards and forwards in the way already described, and which is so much wider on its oral than on its nasal side that it may be compared to a trihedral prism. Transverse sections, however (figs. 3—6, Pl. XXII. [Plate 8]), show that its outline is not quite so simple as that of a trihedral prism would be, its surface being raised into seven longitudinal ridges, separated by as many slight excavations. Of these ridges one is in the middle line above, while the other three lie on each side. Of these the lowermost, situated in the lower and outer part of the maxilla, is very strong and thick, and corresponds with the alveolus of the tusk. The middle lateral ridge is thin and

sharp, and is developed from the maxilla, close to its upper boundary. The supero-lateral ridge is situated on the sides, and the median ridge on the middle, of the premaxillary and nasal bones. The external bony nasal apertures are placed in the upper part of the snout, about $\frac{3}{4}$ths of an inch in front of the orbit; they are irregularly oval, and about an inch long by $\frac{6}{10}$ths of an inch wide. They are $1\frac{1}{2}$ inch apart, but appear to have communicated with one another above the thin bony ethmovomerine septum. In another specimen the bony plate which roofs them in above and in front is wider than in that figured; but in none does it seem to have formed an overhanging ledge.

The extreme termination of the snout is apparently wanting in all my specimens; it was probably curved downwards and convex forwards, but, I suspect, less so than in other Dicynodons. Below the infero-lateral or alveolar ridge, the sides of the maxilla slope abruptly inwards, and are then continued downwards to unite with the palatine bones.

The projecting ends of the tusks are broken off at about two inches from the ends of their fangs in the specimen figured. In the transverse sections (Pl. XXII. [Plate 8] figs. 3–6), it is seen that no trace of the tusk is visible in that taken through the external nostrils (fig. 3); while in that taken $\frac{9}{10}$ths of an inch further forwards (fig. 4), the section of the walls of the tusk, which measures nearly $\frac{7}{10}$ths of an inch in diameter, and has a pulp-cavity $\frac{1}{5}$th of an inch less, is very visible. The pulp-cavity gradually diminishes anteriorly, so that close to where the tusk is broken off, in fig. 6, its diameter is not more than equal to that of its wall, and, as I observe in other specimens, it becomes still less further forwards. The tusks seem to have been nearly straight in this *Dicynodon*, or to have been but very slightly curved.

The occipital bones (Pl. XXIII. [Plate 9] fig. 2) are united into a great vertical quadrate plate, $2\frac{1}{2}$ inches high by $4\frac{1}{2}$ inches broad. The upper edge of this plate exhibits a median notch, on each side of which it passes outwards, nearly horizontally, but with a slight upward convexity, for $1\frac{1}{2}$ inch. It then curves downwards until it joins the lateral face, which at a short distance below the junction presents a deep notch. Down to the level of this notch the occipital surface is nearly flat; but below the notch, it presents an oblique excavation on each side, succeeded by a very strong convexity, whose longitudinal axis is directed downwards and outwards, and which, by its truncated end, apparently abuts against the quadrate bone. The occipital foramen which lies in the midst of the occipital face of the

skull, is shaped like an Egyptian doorway, being high, straight-sided, and wider below than above. It is rather more than $\frac{8}{10}$ths of an inch in height, $\frac{6}{10}$ths of an inch broad at the base, and $\frac{4}{10}$ths of an inch at the summit, which is 1 inch distant from the upper edge of the occipital plate.

I have spoken of this great quadrate bony mass as the "occipital plate," because it appears to me to be formed by the combination of all the elements of the occipital bone. There are traces of the primitive sutures between the basi-occipital and the exoccipitals; but those which should appear between the exoccipitals and supra-occipital are not clearly traceable. On the other hand, there is a very distinct line of separation, which externally becomes a space $\frac{1}{4}$th of an inch wide, between the upper margin of the occipital plate and the body and lateral processes of the parietal. This latter bone has a triangular outline when viewed from behind, measuring fully $1\frac{1}{3}$ inch from base to apex. The union of its lateral processes with the squamosals is distinctly traceable on one side. The parietal process, whose end is rather more than 2 inches from the centre of the bone, passes in front of, and overlaps the inward process of the squamosal.

A strong inferior process or "hypapophysis" is seen descending from the base of the skull on the right side. The quadrate bone is a broad, but comparatively thin, bony plate, $1\frac{1}{2}$ inch wide superiorly and 3 inches long. Its anterior face and its outer edge are convex. The posterior face, which is very concave from above downwards superiorly, and convex in the same direction below, is divided by a vertical ridge into a large outer portion, whose plane is nearly the same as that of the occiput, and a smaller inner division, bent forwards almost at a right angle with the foregoing. The lower moiety of this inner division of the posterior face of the bone is pretty closely applied to the end of the broad process of the exoccipital. The upper moiety forms, with the concave surface of the exoccipital above this process, the lateral walls of a deep fossa, roofed over, above and externally, by the recurved upper part of the quadratum, which is separated from the occipital plate by a small intercalary bone. This appears to me to correspond with that bone called "une espèce d'épiphyse, ou plutôt d'os interarticulaire pour le tympanique," in the Monitor, by Cuvier (Oss. Foss. ed. 2, vol. x. p. 16).

The mandible is imperfect posteriorly; and a considerable part of its symphysial end has also disappeared. It measures about 4 inches as it is, but probably attained between 5 and 6 inches in length when perfect. The depth of the symphysial part of the mandible could

hardly have been less than $2\frac{1}{2}$ inches; and, in the coronary region, the ramus attains about 2 inches in this direction.

The skull whose external characters have just been described is distinguished from those of all hitherto discovered Dicynodons by—

1. The great angle formed by the planes of the intertemporal and facial regions of the upper surface of the skull.
2. The excess of the transverse over the longitudinal diameter of the supratemporal fossæ.
3. The position of the nasal aperture altogether in front of the orbits.
4. The proportional length of the upper jaw in front of the nasal apertures.
5. The length and form of the os quadratum.
6. The circular section and straightness of the tusks;[1] the position of their posterior ends immediately below the nasal apertures; their extension downwards and forwards parallel with the plane of the nasal and premaxillary bones; and their not leaving their sockets till they have passed beyond the level of the posterior end of the symphysis of the mandible.
7. The longitudinal ridges on the prism-like snout.

The Structure of the Skull of Dicynodonts.—The general structure of the Dicynodont skull, so far as it is visible from the exterior, and without making sections, has been fully elucidated by Professor Owen in his papers in the Transactions of this Society (vol. vii.); but no attempt has been made hitherto, so far as I am aware, to work out the anatomy of its deeper-seated parts.

The remarks I am about to offer are the results of my observations upon *Dicynodon Murrayi*, and upon a small skull from the Rhenosterberg, the species of which is not determinable with certainty.

The cranio-facial axis is more completely ossified in *Dicynodon* than in any Reptile I am acquainted with, the presphenoid, the ethmoid and the vomer being, so far as I can observe, entirely osseous.

The basi-occipital is extremely short, and the basi-sphenoid is a very strong cuboidal bone, whose posterior face projects freely, for half its extent, below the basi-occipital. This portion of the bone slopes downwards as well as backwards, and is concave from side

[1] Where the tusks are other than circular in section, their figure is clearly distorted by pressure. It is a curious circumstance, indeed, that no one of the skulls of *Dicynodon Murrayi* which I have seen is free from a certain amount of disfigurement from this cause.

to side. The inferior face, wide but short, is also concave from side to side, but is a little convex from before backwards. The pterygoids abut against the lateral and inferior parts of the basisphenoid.

The presphenoid is united with the basisphenoid by an oblique sutural face: posteriorly it is thick and solid; but anteriorly it thins off into a vertical plate, which extends continuously between the orbits and forms a bony interorbital septum.

The interorbital septum passes into the ethmovomerine plate or nasal septum, which, as far forwards as the front part of the external nasal apertures, is an exceedingly thin but deep plate of bone (fig. 3, Pl. XXII. [Plate 8]). At the anterior boundary of this aperture, however, the upper portion of the nasal septum thickens and rapidly expands into a broad and thick spongy mass, consisting of a horizontal and a vertical portion. The former is $1\frac{1}{4}$ inch wide. Its flat summit articulates with the ascending process of the premaxillary bone; while its obliquely truncated lateral faces, half an inch wide, appear on the face, between the supero-lateral and median-lateral ridges, being interposed between the premaxillary and the maxillary bones, which are completely separated by this horizontal prolongation of the septum narium. The inferior sides of the mass slope downwards and inwards to join the vertical portion of the thickening, which is $\frac{7}{10}$ths of an inch long, by $\frac{6}{10}$ths wide. Its sides are convex, its inferior surface is concave, and from its centre proceeds the thin bony plate which constitutes the proper nasal septum. The maxillary bone unites suturally with the inferior face of the horizontal portion of the bony expansion, and with about the upper half of the outer surface of the vertical portion (Pl. XXII. [Plate 8] fig. 4).

In a section taken nearly an inch further forwards (Pl. XXII. [Plate 8] figs. 5 and 6) the bony expansion has enlarged and acquired a quadrate form, the vertical portion having expanded, so as to be nearly as wide as the horizontal, and uniting throughout the whole of its outer surface with the maxillary bone. Its lateral portions have extended downwards below the level of the alveoli, while the centre of its inferior surface has hardly altered its distance from the anterior, or superior, boundary of the snout. In consequence of this, the inferior surface of the spongy mass forms a deep arch, from whose centre depends the proper nasal or vomerine septum, which has attained a thickness of $\frac{1}{4}$th of an inch.

An inch further towards the end of the snout, no trace of these parts is seen in a transverse section; and I conclude, partly from these sections and partly from other evidence, that the ethmovomerine

plate had a curved inferior margin which ended somewhat abruptly anteriorly, corresponding in all probability with the form of the middle symphysial ridge in the lower jaw. Superiorly it seems to have dilated into a thick bony mass, whose supero-lateral portions intervened between the premaxillary and the maxillary bones, while its infero-lateral parts extended down on the inner side of the maxillary bone, and, as I am inclined from some appearances to think, sent back a process along the maxillary wall, close to the palatine bones, to form a part of the boundary of the internal nares.

The palatine bones are attached to the presphenoid below the anterior boundary of the orbits; they pass, diverging, forwards and outwards, till they reach the lower walls of the maxillæ, into which their upper edges are wedged. Anteriorly, these bones incline inwards and join the lower edge of the ethmovomerine plate. The posterior nares are the two spaces enclosed between them, the palatine bones, and the ethmovomerine septum.

The structure which I have just described cannot, I think, be explained by the analogy of any recent Reptile, nor am I acquainted with any fossil member of the class which presents a similar arrangement of the parts.

In all *Lacertilia*, *Ophidia*, *Chelonia*, and *Crocodilia*, the palatine bone has but a small share in the lateral osseous boundary of the posterior nares; while the vomers or vomer often present a broad inferior surface, and have little vertical expansion.

In the Monitors, however, there is a bony mass, commonly called the turbinal bone, which appears to me to represent very closely the superior expansion of the ethmovomerine plate of *Dicynodon*. Except in proportional size, in fact, it agrees very closely with the latter; for it appears on the upper surface of the skull, between the ascending process of the premaxilla, where it is joined by the descending part of the nasal, and occupies a broad space between the ascending process of the premaxilla and the maxilla, with whose inner and upper edge it articulates. Behind it, the maxilla reaches the prefrontal; in front, the "turbinal" extends inwards to the premaxilla; internally the "turbinal" is continuous with a vertical plate which passes inferiorly into the vomers; and if these bones, instead of being expanded horizontally below, were represented by their thin vertical plate only, the resemblance to *Dicynodon* would be close. But the nasal passages of Birds present a much nearer approximation to those of *Dicynodon*. In such a bird as a Vulture, for instance, the osseous,

vertical vomerine septum expands inferiorly in front of the external nares into a mass of cancellated bone; and that mass bounds the nasal passages in front and above, and sends down a thin septum in the middle line, just as in *Dicynodon.* Furthermore, the posterior nares are bounded externally by the palatine bones to the same extent in the Bird as in *Dicynodon*; and the bone called "inferior turbinal" in Birds occupies a position on the inner side of the palatine and maxillary precisely similar to that occupied by the bone to which I have referred above. Again, the manner in which the palatines and pterygoids are connected with one another and with the presphenoid in *Dicynodon* is extremely bird-like.

Many points in the structure of the mandible and premaxilla are very well shown by the skull of *D. Murrayi* figured in Pl. XXIII. [Plate 9], which displays excellent transverse sections of both the maxillary and the mandibular bones, not only close to the extremity of the snout, where, as I have already mentioned, part of the bony matter is altogether broken away, but at $1\frac{1}{2}$ inch from it, where an accidental fracture has taken place. The inner surface of the premaxillary bones, in front of the septum, is produced into two longitudinal ridges, which have a triangular section, their sharp edges being directed downwards. The upper part of the symphysial region of the dentary element of the mandible is developed into three very strong processes which fit into the interspaces left between these ridges—at the sides, and in the middle between each ridge and the downwardly inclined sides of the premaxilla.

The median ridge is $\frac{3}{4}$ths of an inch high and $\frac{1}{3}$rd of an inch thick at its base. It expands superiorly and ends in a sharp edge, so that its section is lancet-shaped. It is separated by a deep groove from the lateral plates, which are slightly curved, not so long as the median plate, and are obliquely bevelled off internally. A section of either ramus shows that the upper edge of the dentary bone in this region is broad and produced into a thick inner and a thin outer wall, separated by a deep groove, which, in consequence of the convexity of its walls, is much narrower below than above. Inferiorly the dentary bone sends down a broad plate on each side. The inner of these remains comparatively thin and comes into contact with the splenial element; the outer becomes very thick where it passes the longitudinal ridge which marks the outer surface of the dentary bone, and then, thinning, overlaps the supra-angular element. The dentary element extends back for more than half the length of the ramus In almost all these respects the dentary bone of *Dicynodon* is very

Chelonian, as will be obvious to any one who compares with these the corresponding sections of a Turtle's mandible. The splenial bone, however, appears to extend to the symphysis, where it unites with its fellow.

A fragmentary specimen of the skull of a small *Dicynodon Murrayi* exhibits very beautifully marked impressions of the sclerotic bones in their natural arrangement. They form a zone $1\frac{6}{10}$ inch in diameter and $\frac{1}{2}$ an inch broad, which closely adapts itself to the bony circumference of the orbit. The sclerotic ring does not seem to have consisted of more than four or five ossicles.

Bones of the Extremities of D. Murrayi.—The only complete bone of the extremities which I have met with is a left humerus (Pl. XXIII. [Plate 9] fig. 3) $3\frac{6}{10}$ inches long, and not unlike that of a *Monitor*, except that it is proportionally wider at the articular ends and narrower in the middle. The deltoid crest is very large, with an almost semicircular free margin; and there is a deep posterior intercondyloid depression, as if for a large olecranon-process.

Among the other remains, I found an extremely interesting fragment, consisting of the anterior part of the sacrum and the last dorsal or lumbar vertebra of *Dicynodon Murrayi.*

The lumbar vertebra is biconcave; its centrum measures $\frac{7}{10}$ths of an inch antero-posteriorly and an inch transversely at its ends, while its centre is a little constricted. Superiorly it widens, and, uniting with the base of the neural arch, enters into a broad but short transverse process. The neural arch is broad, thick, and depressed,—the neural canal not exceeding $\frac{3}{10}$ths of an inch in diameter. A strong spinous process rises from it, and passes obliquely upwards and backwards for an inch, to end in a truncated extremity. The first sacral vertebra is like the last lumbar; but the lateral enlargement, or rudimentary process, into which the neural arch and the centrum enter, unites suturally with the smaller end of a broad fan-shaped pleurapophysis, $\frac{3}{4}$ths of an inch long, whose outer, vertically expanded, obliquely truncated end abuts against the inner surface of the ilium. The centrum of this vertebra is $\frac{4}{5}$ths of an inch long, and it is concave anteriorly, flat posteriorly. The anterior articular face of the centrum of the next sacral vertebra is also flat, and is closely applied to, if not partially anchylosed with, the flat hinder face of the first. The upper parts both of it and of the next vertebra are much mutilated, but their pleurapophyses, similar to, but smaller than, those of the first sacral, are well preserved. The anterior faces of these

pleurapophyses look downwards as well as forwards. The fragment of the ilium shows that this bone was very broad and expanded, concave externally, slightly convex internally, and much thicker towards its ventral than at its dorsal edge.

DESCRIPTION OF PLATE XXIII. [Plate 9].

Fig. 1. Lateral view of the skull of *Dicynodon Murrayi*. Reduced to one-half diam. The fossil has been accidentally fractured in the direction *a b*.

Fig. 2. The same skull, viewed from behind; reduced to one-third diam.

Fig. 3. The left humerus (nat. size) of a *Dicynodon Murrayi*.

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3

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Vest del & lith

DICYNODON MURRAYI

VIII

ON RHAMPHORHYNCHUS BUCKLANDI, A PTEROSAURIAN FROM THE STONESFIELD SLATE

Quarterly Journal of the Geological Society, vol. xv., 1859, *pp.* 658–670.
(*Read March 23rd*, 1859.)

PLATE XXIV. [PLATE 10].

SINCE the description of the fossils belonging to this species of Pterosaurian which originally came into my possession, I have met with so much additional material, that I have thought it better completely to remodel the present Memoir, than to add the subsequently acquired information in cumbrous notes.

Some time ago, the Earl of Ducie was good enough to place in my hands, for description, a portion of a lower jaw, about $3\frac{1}{2}$ inches in length, which was obtained from a quarry known by the name of "Smith's Quarry," at Sarsden, near Chipping Norton, in Oxfordshire. Bones of Pterosaurians abound in this locality, associated with remains of *Megalosaurus* and of Oolitic fishes; and Lord Ducie considers that the beds in which his fossil was discovered are the representative of the Stonesfield slate. In this conclusion, I find, my colleagues of the Geological Survey concur.

The symphysial part of the lower jaw in question, and the whole of what remains of the right ramus, are extremely well preserved (Pl. XXIV. [Plate 10] figs. 1*a*, 1*b*); but the inferior part of the left ramus is broken away at a distance of about an inch behind the symphysis. The latter measures $\frac{7}{8}$ths of an inch in length, and exhibits no suture. Its posterior boundary is nearly a quarter of an inch thick, and looks downwards as well as backwards.

The distance between the two edges of the rami opposite the posterior extremity of the symphysis is $\frac{15}{16}$ths of an inch, the depth of a ramus measured perpendicularly at the same point being $\frac{7}{16}$ths of an inch. The outer faces of the rami are here inclined at an angle of 45° to a vertical longitudinal plane; and they converge to a rounded edge, which forms the lower margin of the symphysis, and bends upwards anteriorly, so as to exhibit a slight downward convexity. In front, the symphysis ends in the base of a stout median process, whose continuation is unfortunately fractured. Its section is an elongated oval with rather sharp extremities, having its greater diameter about $\frac{5}{16}$ths of an inch long and vertical. Its transverse lesser diameter measures $\frac{1}{4}$ of an inch. It is obvious, from what remains of the upper and lower contours of this beak-like process, that it was curved and prolonged upwards and forwards. Its walls are exceedingly thin, and the cavity which it contains is filled with a partially crystalline matrix.

Immediately behind the base of this rostrum the ramus of the mandible suddenly deepens to $\frac{5}{8}$ths of an inch, the chief increase in diameter being due to the projecting edges of two large, transversely oval alveoli, each nearly $\frac{1}{4}$ inch wide, which are directed forwards and outwards on either side.

Behind these alveoli the jaw narrows a little, but at $\frac{3}{8}$ths of an inch from their posterior boundary deepens once more to $\frac{7}{8}$ths of an inch. A second equally large alveolus, which also looks forwards, outwards, and upwards, occupies the posterior part of the concave interspace in front of this second deepening on each side. After a second slight contraction, the lateral margin of the jaw rises again opposite the symphysis, where the ramus has the dimensions given above. Just behind the line of the symphysis is another oval alveolus of the same length, with a slightly more outward and less forward direction.

Three-eighths of an inch from the posterior margin of this third alveolus is a fourth, of about the same size; and after a similar interval a fifth alveolus follows,—the sinuation of the margin between the two last alveoli being much less marked. The interval between the upper edges of the two rami at the level of the last alveolus, which is about $1\frac{3}{16}$ inch behind the posterior edge of the symphysis, is $1\frac{1}{4}$ inch.

From the hinder margin of the last alveolus of the posterior extremity of the fragmentary ramus is a distance of $1\frac{1}{4}$ inch; and the distance between the fractured ends of the two rami is $1\frac{1}{2}$ inch.

Posteriorly, the rami of the mandible not only narrow to a depth of $\frac{3}{8}$ths of an inch, but their planes gradually become vertical. The section of the ramus is a long oval, the width of which is not equal to more than a third of its length; and its bony substance is, here as elsewhere, extremely thin.

There is not the slightest trace of an alveolus behind the fifth; and the sutures which ordinarily mark out the components of a reptilian mandible are not visible on either the outer or the inner faces of the rami.

The fang of a tooth is lodged in the third alveolus on the right side; and an entire tooth remains in the fifth alveolus of the same side. A similar tooth is much better displayed on the left side, implanted in the fifth socket, and directed upwards, forwards, and outwards. The total length of this tooth is about $\frac{15}{16}$ths of an inch. Its exserted portion, or crown, is twice as long as the root, and is straight and flattened from side to side, tapering gradually to a sharp point. Where it leaves the alveolus, the tooth measures $\frac{3}{16}$ths of an inch in diameter. The surface of the crown is smooth and devoid of ridges or folds,—the short, irregular, close-set, longitudinal striæ with so much of the enamel-like outer layer as is preserved presents, seeming to be mere cracks.

The extreme thinness of the bony walls of this mandible, the mode of implantation and the form of its teeth, clearly prove, as Lord Ducie had discerned, its Pterosaurian nature; and the prolonged symphysial beak further demonstrates its relations with that group of *Pterosauria* called "Subulirostres" by Von Meyer, and thus described by that eminent palæontologist:—

"The anterior end of the jaw passes into an edentulous point, on to which a horny beak was probably fitted; the eye had probably no osseous ring;[1] the scapula and coracoid are anchylosed;* and the tail is long and stout."—*Palæontographica*, vol. i. p. 20.

I am indebted to Mr. Rupert Jones for bringing under my notice two other Pterosaurian mandibles found in the Stonesfield slate itself. One of these, a very perfect and beautiful specimen, but unfortunately devoid of teeth, belongs to Professor Quekett, of the Royal College of Surgeons; the other, consisting of a portion of a right ramus, forms a part of the collection of this Society.

In the first of these specimens (Pl. XXIV. [Plate 10] fig. 2) the left ramus is completely exposed; and the fossil is so broken at about the junction of its anterior and middle thirds, as to display

[1] The characters marked * have been shown by subsequent investigations not to be constantly associated with the other peculiarities of *Rhamphorhynchus*.

in transverse section, not only this ramus, but its fellow of the opposite side.

The left ramus is $4\frac{1}{3}$ inches long. The posterior portion of its inferior edge is nearly straight; but it becomes curved anteriorly, so as to have a slight downward concavity. Beneath the two anterior alveoli the concave curvature sweeps into a somewhat decided convexity; and in front of a line drawn through the anterior alveolus, the lower contour of the mandible is prolonged forwards and upwards into the inferior margin of the rostrum, in which the extremity of the mandible ends.

The superior edge is, for the most part, slightly convex upwards, but anteriorly it exhibits a slight concavity, while posteriorly, or near the articular end, it suddenly curves downwards and backwards. It is rendered slightly sinuous by the projection of the margin of the alveoli.

The angle of the jaw is formed by a thin and short process, rounded off posteriorly, which projects for about $\frac{1}{6}$th of an inch behind the posterior edge of the articular cavity, and has about the same depth, if measured along a perpendicular line drawn immediately behind that edge.

The articular cavity itself is about $\frac{1}{6}$th of an inch long. It is concave upwards; and its anterior margin is so much higher than the posterior, that a line joining the two, slopes gradually upwards into the convexity of the coronary region. The cavity is somewhat broader than it is long; and its anterior and posterior boundaries converge internally, so that it has the form of a triangle with its base turned outwards. The posterior boundary passes into the thin angular process, the anterior into the still thinner coronary part of the jaw. This part attains its greatest elevation about ·7 inch from the angle of the jaw, the depth of the mandible being at this point ·4 inch.

There are altogether seven alveoli, the hindmost of which is an inch and a half distant from the angle of the jaw. This alveolus measures rather more than $\frac{1}{6}$th of an inch in length; the others are about $\frac{1}{5}$th of an inch long, or a little more; the second and third are largest; and all are oval. The posterior edge of the sixth alveolus (counting from before backwards) is 1·9 inch from the angle of the jaw; of the fifth, 2·3 inches; of the fourth, 2·8 inches; of the third, 3·1 inches; of the second, 3·5 inches; of the first, 3·8 inches. When the rostral end of the mandible was entire, the whole length of the ramus was probably very little under five inches, as the rostrum must have extended fully ·6 inch beyond the

first alveolus. The vertical diameter of the ramus is least between the fifth and sixth alveoli, where it amounts to about $\frac{7}{20}$ths of an inch. Anteriorly the vertical diameter increases to the second alveolus, where it measures half an inch.

The upper edge of the rostrum is nearly straight. Its obliquely broken end has an oval section, measuring $\frac{1}{5}$th of an inch vertically by $\frac{1}{20}$th horizontally. The specimen has been broken through immediately behind the third alveolus; and the section of the left ramus at this point has the form of an elongated oval, half an inch long by one-tenth of an inch wide. The plane of the ramus is directed a little outwards, as well as upwards; and its walls are extremely thin. The fractured surface of the matrix further exhibits a sectional view of the right ramus, whose plane is similarly inclined, so that, while the lower edges of the two rami are only $\frac{1}{5}$th of an inch apart, the upper edges are more than $\frac{1}{3}$rd of an inch distant.

The outer surface of the left ramus exhibits, nearer the lower than the upper margin, and extending from the level of the fourth alveolus to that of the anterior margin of the second, a slight horizontal ridge. This ridge terminates abruptly in front, and seems to have constituted the outer wall of a vascular canal; for a delicate groove is continued forwards from it, and vanishes upon the outer surface of the bone. Other canals of a similar character are seen upon the rostrum. These vascular ramifications are so similar to those observable upon that portion of a bird's bony jaw which is covered by the horny beak, that I should have been inclined to suspect the existence of a similar horny sheath to the mandible, even had not Von Meyer demonstrated its existence in *Rhamphorhynchus Gemmingi*.

The sutures which should limit the different components of the jaw are very indistinct. The best-marked runs obliquely from below the articular cavity, upwards and forwards, to a point half an inch in advance of the anterior edge of that cavity, and $\frac{1}{5}$th of an inch below its upper margin. Here it ends in a minute pit filled with matrix. Another less distinct, apparently sutural, line is traceable from immediately behind the last alveolus backwards, to a point nearly midway between the pit just mentioned and the anterior edge of the articular cavity. Here it is joined, at an acute angle, by another indistinct line coming from the pit; and the two enclose a triangular tongue of bone. I suspect that this belongs to the dentary element, and that the pit answers to the foramen visible on the outer face of the Crocodile's jaw, between the supra-angular, angular, and dentary elements.

The fossil in the Society's Museum (Pl. XXIV. [Plate 10] fig. 3) consists of a right ramus whose anterior end is broken off, the remaining part measuring 4 inches in length. The angle of the jaw is a little broken, and extends for hardly more than $\frac{1}{6}$th of an inch behind the posterior margin of the articular cavity. The latter is fully $\frac{1}{5}$th of an inch long; and the coronary margin, in front of it, slopes upwards much more gradually than in the last-described specimen, so that the greatest vertical diameter of the mandible (0·65 inch) is $1\frac{1}{5}$ inch distant from the anterior edge of the articular cavity.

From this point the upper margin of the mandible declines but very little towards the hindmost alveolus, where the depth of the ramus is $\frac{3}{5}$ths of an inch. The hinder edge of this alveolus, which is oval and $\frac{1}{5}$th of an inch long, is distant 2·35 inches from the anterior edge of the articular cavity. A second alveolus, of about the same size, is situated $\frac{1}{2}$ an inch in front of the last; and a third, rather larger, is $\frac{1}{4}$th of an inch in advance of the penultimate one. The inferior margin of the ramus is very slightly curved; and its vertical diameter, in front of the antepenultimate alveolus, is 0·55 inch. The section here exposed is oval, and about $\frac{1}{6}$th of an inch wide in the middle.

The outer surface of the ramus exhibits very nearly the same sutural markings as in the preceding specimen. The "pit," however, is one inch in front of the anterior margin of the articular cavity.

The two last-described specimens came under my notice only on the day on which I described the first to the Society; and I was then inclined to refer all three to one species; but having since been enabled to submit them to a much more careful examination, and to clear away so much of the matrix as obscured any doubtful points, I see many difficulties in the way of adopting that conclusion.

Taking the most perfect of these fossils, or that belonging to Professor Quekett, as the type, I find, on a close comparison with the Sarsden specimen, that, although the proportions of the two, even down to the intervals of the teeth, are so similar that they might have belonged to individuals of very nearly the same size, there are many differences. The Sarsden mandible is altogether more robust; the planes of the rami, which are thicker, are more inclined outwards. The rostrum is not quite so deep in front of the first alveolus. The lower margin of the mandible is much less curved; and I can find no trace of the horizontal ridge or the vascular ramifications. I am not disposed to lay so much weight on

these discrepancies, however, as on another fact, viz., that I cannot discover the least trace of any alveolus behind the fifth, in either ramus of the Sarsden species, although on the right side more than an inch of the ramus is preserved behind the fifth dental socket, and although on the left side the ramus is so broken away that any remains of a tooth, or of the alveolus in which it was lodged, could hardly fail to be visible.

If the differences which I have indicated should prove to be constant, I would propose for Lord Ducie's fossil the name of *Rhamphorhynchus depressirostris.*

The ramus in the Society's Collection also differs more than I at first imagined from that belonging to Professor Quekett. The distance from the anterior margin of the articular cavity to the posterior margin of the hindmost alveolus is, in the latter, to the like measurement in the former, as 13 to 23. The distance of the "pit". from the anterior margin of the articular cavity and from the last alveolus, in the two cases, is in about the same proportion; but the depth of the jaw is not in the same ratio, nor is the space occupied by the three corresponding alveoli; and in the Society's specimen the highest part of the coronary region is far more forward than in the other. If, however, we are to be guided by the proportions first stated, the mandible in question must have been between nine and ten inches long, and the differences observed might be accounted for by the different ages of the animals whence the parts compared were derived. As I am not aware of any evidence tending to show the nature of the variations undergone by the mandibles of the *Pterosauria* in their progress from youth to age, I must leave open the question of the specific identity of Professor Quekett's specimen with that in the museum of the Geological Society.

It will be understood that I regard the former as the typical Stonesfield Pterosaurian; and I now proceed to compare it with the known remains of other *Rhamphorhynchi.*

To the four species referred to *Rhamphorhynchus* by Von Meyer, viz. *macronyx*, *Muensteri*, *Gemmingi*, and *longicaudus*, Professor A. Wagner, in a recent very valuable memoir,[1] adds *longimanus*, *curtimanus*, *hirundinaceus*, *crassirostris*, and *Banthensis*, making nine species in all. Wagner considerably adds to and amends the definition of *Rhamphorhynchus* given by Von Meyer. Thus, while in the *Pterodactyli* proper the cranium exhibits on each side only two

[1] Neue Beiträge zur Kenntniss der urweltlichen Fauna des lithographischen Schiefers. Erste Abhandlung: Saurier. Abhand. d. König. Bayerischen Akademie, viii. (1858.)

cavities enclosed by bone (the orbits and the nasal apertures), the *Rhamphorhynchi* have a third cavity interposed between the nares and the orbits; and they may possess a sclerotic ring. Their teeth, which are very long and curved, only the foremost and hindmost being short, do not reach the anterior end of the premaxilla and mandible, but they extend back to the orbits. The tail is very long, far surpassing in length the rest of the vertebral column, and consisting of more than 30 vertebræ, which are at first short, but rapidly elongate, retain their length for a considerable distance, and then gradually diminish. The caudal vertebræ, with the exception of the most anterior, which remain movable, are immovably united together by long bony fibres, externally invested by a firm sheath, so that the tail is always stiffly extended. Furthermore, according to Wagner, the cervical vertebræ of the *Rhamphorhynchi* are as broad as they are long, the dentata forming the only exception to this rule. The coracoid and scapula may be anchylosed or otherwise. The fourth metacarpal bone is always far shorter than half the length of the fore-arm.

The *Rhamphorhynchi* have already undergone a further subdivision by the separation, as a distinct genus, of the Liassic *R. macronyx*[1] of our own country. The specimen of that species originally obtained and described by Dr. Buckland is, as is well known, devoid of the head; but Professor Von Meyer's observations on German specimens, made and published so long ago as 1846, supplied this deficiency, so far as the lower jaw is concerned:—

"Behind the sharp, upwardly-bent, edentulous point of the lower jaw, there are on each side, as far as the symphysis extends, three large teeth set at a certain distance from one another. To these succeed a series of close-set oval alveoli for smaller teeth, which are situated upon the separate rami of the mandibles, and are numerous."[2]

Von Meyer's discovery of the remarkable characters of the dentition of *Rhamphorhynchus macronyx* has been confirmed by a specimen which has recently come to light in this country, and has been described by Professor Owen under the name of *Dimorphodon*. I am not aware that this description (which, as I am informed, was read before the British Association at its last meeting) has yet been published;[3] but as the specimen forms a part of the collection of the

[1] Geol. Trans. 2 ser. vol. iii. p. 217, pl. 27.

[2] Palæontographica, vol. i. p. 6.

[3] The abstract of Professor Owen's Memoir, now published in the Report of the British Association for 1858, contains a full account of the dentition of *Dimorphodon*, and must, of course, be considered to have priority over any statement on the subject in the text, which I

British Museum, I have been enabled to inform myself fully as to its characters.

The symphysis of the mandible is broken through, the anterior end of the right ramus lying considerably behind that of the other branch of the jaw; and the extremities of both rami are broken; hence it is impossible to say in what way they terminated. The anterior end of the right ramus, however, exhibits three strong teeth, which, where perfect, project rather less than $\frac{1}{2}$ an inch above the alveolar margin, and are separated by intervals of about $\frac{3}{8}$ths of an inch. The anterior of these teeth is recurved; the second is straight, conical, and pointed; and so much as remains of the third seems to show that it had a similar figure.

Immediately behind the third large tooth commences a series of very minute teeth, nearly fifty in number, and occupying a space $2\frac{13}{16}$ inches long. Three-quarters of an inch behind the last, there appears to be the remains of another straight lanceolate tooth; but I am not quite certain that this is the case. Only two of the large teeth are visible in the left ramus; and there is no means of telling how far the symphysis extended. Behind the second tooth the ramus is half an inch deep, and it becomes gradually wider, until posteriorly it is three-quarters of an inch deep. Its bony walls appear to have been extremely thin and flat; but they are strengthened by a prominent longitudinal shelf-like ridge, which is developed from the inner surface of each ramus about a quarter of an inch from its inferior edge.

It is obvious from this brief description, that, notwithstanding certain similarities, the mandibles of the *Rhamphorhynchi* from Sarsden and Stonesfield are extremely different from that of *Dimorphodon macronyx*.

On the other hand, the proportions of the Stonesfield and Sarsden mandibles, the form of their rostrum, and the straightness of the only teeth which are preserved, appear, if I may judge from the figures and descriptions which have been published by Goldfuss, A. Wagner, and Von Meyer, to separate them no less distinctly from the other known species of *Pterosauria* belonging to this division.

The Pterosaurian remains which were obtained from the Stonesfield slate many years ago by the late Dr. Buckland, and are now

leave standing merely because it formed a part of my original communication, and because, with Von Meyer, I find three, and not two, long prehensile teeth in the fore part of the right ramus of the mandibles. The greater part of the third tooth, however, is broken away; and its stump became clearly visible only upon removing a small portion of the matrix. —Dec. 1859.

deposited in the Geological Museum in Oxford, have neither been figured nor described, though Goldfuss invented for them the name of *Pterodactylus Bucklandi.* When in Oxford a short time ago, I had the opportunity (thanks to the kindness of our President, the Curator of the Museum) of examining these remains; and in the course of my somewhat hasty inspection, I noted, among fragments of less moment,—

1. A right humerus (Pl. XXIV. [Plate 10] fig. 7), $3\frac{1}{2}$ inches long, and $1\frac{1}{2}$ inch in diameter at its proximal end, which terminates internally in a rounded articular head, more than half broken away, but seemingly about $\frac{1}{4}$th of an inch thick, and externally is prolonged into a thin but strong process with rounded edges, whose anterior or proximal margin is decidedly concave. The proximal end of the shaft is flattened; but it becomes rounder, concave anteriorly and convex posteriorly, towards its distal end. This last is about $\frac{5}{8}$ths of an inch wide, and strongly bent forwards, its plane forming an angle of about 45° with that of the proximal end of the bone. [The right humerus of the original specimen of *Dimorphodon macronyx* lies in nearly the same position as this, and may be advantageously compared with it.]

2. A right coraco-scapular bone, similar to, but smaller than, that which will be described below,—the coracoid measuring only $2\frac{1}{2}$ inches in length, and the scapula $2\frac{1}{8}$ inches from the suture, which is visible half an inch above the lower edge of the coracoid.

3. A distal phalangeal bone of the fourth, or web-finger, $6\frac{1}{2}$ inches long. This bone is nearly $\frac{3}{16}$ths of an inch thick at its proximal end, where it is somewhat flattened from side to side. In the middle it becomes rounded, and remains so, gradually tapering to its slender distal end, which is a little flattened from side to side, and rounded off at its extremity, which looks like a natural termination. The bone is straight for the proximal $4\frac{1}{2}$ inches of its length; it then becomes slightly curved, so as to be convex forwards, and concave backwards, in the rest of its length.

4. A fragment of a proximal phalanx of the same finger, embracing probably more than its proximal half, three inches long. The shaft of this bone is $\frac{7}{16}$ths of an inch thick; its head, including its anterior process, measures more than an inch antero-posteriorly and its articular cavity is rather more than $\frac{1}{2}$ an inch in diameter.

5. A middle (2nd?) phalanx, $7\frac{3}{4}$ inches long, and $\frac{1}{2}$ an inch wide at its proximal end.

6. Another middle (3rd?) phalanx of about the same length, but more slender.

7. An abdominal rib.

8. The proximal end of a rib, apparently Pterosaurian, with a distinct capitulum and tuberculum.

Out of the great number of detached teeth from Stonesfield in the Oxford Collection, I could find none of *Pterosauria*, nor is there a fragment of a mandible.

In the Collection of the Royal College of Surgeons there are several Pterosaurian remains from Stonesfield named *P. Bucklandi*: among them is a proximal phalanx of the long finger, $7\frac{3}{8}$ inches long; a left external metacarpal, $1\frac{3}{4}$ inch long; and a bone which is described by Professor Owen in the 'Catalogue' as a tibia.

From what I have just stated, it is obvious that it is impossible to compare the mandibles I have described with the corresponding parts of the species named *Pterodactylus Bucklandi*, inasmuch as none such exist; but, since a specific name published without a description has no authority, I shall not hesitate to affix the name of *Rhamphorhynchus Bucklandi* to the nearly perfect mandible from Stonesfield, and, provisionally, to the other remains from the same locality. If, however, it should turn out that the separation of the Sarsden mandible as a distinct species is necessary, it will be a further question to determine to which of the two mandibles the other bones respectively belong. For the present I will speak of them all as remains of *R. Bucklandi*.

I have seen no vertebræ from Stonesfield, nor any part of the skull or pelvis. There is, however, in the Museum of Practical Geology a very well preserved coraco-scapular bone (Pl. XXIV. [Plate 10] fig. 4). This fossil was presented, among other bony fragments from the Stonesfield slate, by the late Marchioness of Hastings. The bone was originally greatly obscured by the matrix; but on clearing the latter away with great care, I brought to view a considerable portion of the right pectoral arch of a Pterodactylian reptile of considerable dimensions. The coracoid bone is almost entire; but only a small portion of the scapula remains.

The coracoid measures $3\frac{3}{16}$ inches in length; but it was probably $\frac{1}{8}$th of an inch longer, as the extremity of its anterior process is broken off.

In the middle of its length, its section is nearly circular and $\frac{1}{4}$th of an inch in diameter; but anteriorly (or externally) it becomes flattened from side to side, while posteriorly (or internally) it also becomes flattened, but in a plane at right angles to that of the anterior end. Its posterior extremity attains half an inch in width;

but its edges are broken and rounded off, and it was probably much wider and abruptly terminated at the end.

The upper (or posterior) surface is a little concave from side to side; the lower (or anterior), convex. The inner edge is thick and rounded; the outer, thinner. The anterior portion of the coracoid is wider below than above, its anterior inferior edge being produced outwards into an elongated tuberosity, which causes the outer face of this part of the bone to appear concave from above downwards, and the more so as the anterior upper part of the bone is equally produced to form the lower boundary of the glenoid cavity for the humerus. The anterior and inner part of the coracoid is elongated into a short process, whose extremity is broken off.

The anterior extremity of the coracoid bends up at right angles to the rest of the bone, to form a very stout bony mass, $\frac{5}{8}$ths of an inch thick, which passes without a trace of suture into the scapula. This perpendicular scapulo-coracoid portion of the bone measures $1\frac{3}{8}$ inch from the lower edge of the coracoid, is half an inch thick from side to side, and about the same antero-posteriorly. The glenoid cavity is situated on the anterior half of its outer face, is concave from above downwards, and would appear to be much more so if its projecting upper and lower boundaries were not broken off; it is convex from side to side; and if the coracoid be held horizontally and with its long axis directed antero-posteriorly, it looks forwards and outwards, while its axis is directed downwards, forwards, and inwards. Only a very small fragment of the scapula remains above the glenoid cavity; it does not present a sufficiently determinate form to be worth description.

I should not have felt so confident in my determination of the nature of this part, had it not been for the clear manner in which the structure of the coraco-scapular arch is to be seen in the original specimen of *Dimorphodon macronyx*, to which I have already referred.

As Dr. Buckland's description of these parts is very brief,[1] and as, with the aid and permission of my friend Mr. Waterhouse, I was able to relieve them more extensively, and thereby develop some important and hitherto unnoticed peculiarities of structure, it may be useful if I describe the left coraco-scapular apparatus in *D. macronyx*, which is now very perfectly displayed in the original specimen in the British Museum (Pl. XXIV. [Plate 10] fig. 6).

The coracoid bone is $1\frac{3}{4}$ inch long. Its anterior end is thick and strong, and compressed from side to side. Below the glenoid cavity, its outer face is nearly plane from before backwards, but is concave

[1] Geol. Trans. 2nd ser. vol. iii. p. 221.

from above downwards. Its contour is, roughly, that of a right-angled triangle with its apex directed backwards; and its lower edge passes into the sharp, outwardly concave ridge, into which the outer side of the posterior half of the coracoid is produced. Anteriorly, this lower edge rises into a rounded ridge-like tuberosity, as in the preceding species.

The anterior end of the coracoid is produced for about half its depth into a process which appears to have been short, but whose extremity is covered by the adjacent humerus. So much of this process as can be seen is not more than $\frac{1}{8}$th of an inch long. At its superior angle, the outer surface of the anterior end of the coracoid is raised into a strong and prominent, somewhat sharp-edged ridge, which forms the lower lip of the glenoid cavity.

The posterior extremity of the coracoid is fully half an inch wide, and is thicker in the middle than at either angle. The inner angle, again, is thicker than the outer, and more produced. The walls of the coracoid are as much as $\frac{1}{16}$th of an inch thick in the middle of the shaft; so that its parietes are proportionally thicker, and its cavity less, than in the bones of the extremities, or of the jaws. This is intelligible when we consider that, in the absence of clavicles, the coracoid must have sustained the thrust of the downward stroke of the fore-limb, and the concomitant strain of the pectoral muscles.

Thus, the sternal end of the coracoid is, as in Birds, flat, expanded, and much wider than the middle, rounded part of the shaft of the bone, while its humeral end is thickened and elongated vertically. The plane of the sternal end does not form a right angle with that of the humeral end, but cuts it obliquely, passing upwards as well as outwards.

The glenoid cavity is about $\frac{1}{4}$th of an inch long, and looks obliquely forwards and outwards, in the position in which the bone is figured; but in all probability it looks backwards and outwards in the natural position. It is wider at each end than in the middle, and above than below; it is concave from above downwards, and convex from side to side.

Superiorly, the humeral end of the coracoid passes into the scapula without any visible suture. The scapula becomes flattened from before backwards, above the upper edge of the glenoid cavity, where it has a width of about $\frac{1}{4}$th of an inch. Its general direction is at an angle of about 60° with the coracoid; but it is slightly curved, so as to be convex forwards and concave backwards.

Its thickness is greatest along its axis; and both edges are thin. Its precise form and dimensions at its posterior end cannot be

ascertained, as this part of the bone is partially crushed by the superjacent radius and ulna. The total length of the scapula is rather more than two inches.

From the close similarity in form and proportions between so much of the coraco-scapular arch of the Stonesfield specimen as is preserved and the corresponding parts of the same apparatus in *Dimorphodon macronyx*, there can be little doubt that it is tolerably safe to complete the outlines of the former in accordance with the indications given by the latter, the sternal end of whose coracoid must therefore have measured $\frac{7}{8}$ths of an inch in width, while its scapula must have been more than four inches long.

The coraco-scapular bone in the Oxford Museum, to which I have referred above, is hardly more than half as large as that represented in fig. 4. It is exposed from its inner side; and the short and rounded anterior coracoid process is well displayed. The plane of the scapula is inclined at nearly $45°$ to a vertical plane traversing the longitudinal axis of both bones. The bone itself is thicker in the middle than at the edges, which are sharp; and it is considerably expanded from before backwards below, where it unites with the coracoid. The internal face of the latter bone is flattened and slightly concave from above downwards anteriorly; but posteriorly, or inferiorly, it presents a thick edge, convex from above downwards, and slightly concave from before backwards.

A specimen from the Stonesfield slate, for which I am indebted to Dr. Wright, exhibits a left coracoid with a small portion of the scapula, from the inner side (fig. 5, Pl. XXIV. [Plate 10]). It shows the coraco-scapular suture and the thick inner edge of the coracoid very well. The extreme end of the coracoid is absent; but what remains of this bone is three inches in length, so that it can have been but little inferior in size to the largest described above.

There are in Dr. Wright's Collection some incomplete bones which appear to be portions of humeri; and he has one very fine and nearly perfect metacarpal of the long finger of the left fore-limb. This bone (Pl. XXIV. [Plate 10] fig. 8) is fully two inches long. Its trochlear distal extremity, which is somewhat bent downwards, is half an inch wide, and is divided by a deep excavation or groove into two portions, of which the inner is rather the larger. This groove is continued a little way backwards on the dorsal surface of the shaft of the bone, which is flattened, and about $\frac{3}{16}$ths of an inch wide by $\frac{1}{5}$ inch thick. Posteriorly, or proximally, the bone rather suddenly widens to $\frac{6}{16}$ths of an inch; and the wide surface exhibits the commencement of the two grooves separated by a ridge, which are

characteristic of it. Looking at the bone as a whole, the inner margin is concave anteriorly, straight posteriorly; while the outer margin is straight or a little convex anteriorly, and concave posteriorly.

The Rev. Mr. Witt has also very obligingly permitted me to examine his collection of Pterosaurian bones and teeth from Stonesfield. In addition to many fragments of finger-bones, it contains the shafts, with their articular ends broken off, of several humeri, the largest of which must have been nearly the size of that in the Oxford Museum. Besides this, there is the moiety of a proximal phalanx of the long finger (Pl. XXIV. [Plate 10] fig. 9), which displays very well the character of the proximal articular end of that bone; and there are among the teeth, almost all of which are those of *Teleosauria*, two long, curved, and pointed ones, which, from the absence of striæ on their surface, and their general characters, I suspect to be Pterosaurian.

It is possible to form an estimate of the minimum size of the Stonesfield Pterosaurian, on the assumption that all the remains which have been described are of one species; for, as all the bones of the long finger and its metacarpal have been obtained, it is clear that the finger and the hand must have been at least as long as the sum of the measurements of these detached bones. Now, as there is a

Distal phalanx	$6\frac{1}{2}$ inches long	
3rd phalanx	$7\frac{3}{4}$ " "	
2nd phalanx	$7\frac{3}{4}$ " "	
Proximal	$7\frac{3}{8}$ " "	
Metacarpal	2 " "	it is clear

that finger and hand attained at least $31\frac{3}{8}$ inches in length.

Then, as in *Rhamphorhynchus* the fore-arm is more than twice as long as the metacarpal, and as there is a humerus $3\frac{1}{2}$ inches long, 40 inches will not be far from the length of one wing, and 7 feet may be safely assumed as the minimum distance between the extremities of the two wings, of the largest *Rhamphorhynchus Bucklandi*, any of whose remains have yet been found.

DESCRIPTION OF PLATE XXIV. [PLATE 10].

Fig. 1 *a*. Part of the mandible of a *Rhamphorhynchus* (*Bucklandi*, or *depressirostris*) in Lord Ducie's Collection, viewed from below.

Fig. 1 *b*. The same, viewed from the side and below.

Fig. 2. Right ramus of a mandible of *Rhamphorhynchus Bucklandi*, in Professor Quekett's Collection.

Fig. 3. Part of the mandible of *Rhamphorhynchus Bucklandi* (?), in the Museum of the Geological Society.

Fig. 4. Part of the coraco-scapular bone in the Museum of Practical Geology.

Fig. 5. Internal view of a left coracoid, with part of the scapula, of *Rhamphorhynchus Bucklandi* (?), in Dr. T. Wright's Collection.

Fig. 6 *a*. Entire coraco-scapular bone of *Dimorphodon macronyx*, in the British Museum.

Fig. 6 *b*. Outline of the proximal end of the coracoid.

Fig. 6 *c*. Profile of the glenoid cavity.

Fig. 7. A right humerus of *R. Bucklandi* (?), in the Geological Museum of Oxford.

Fig. 8. Dorsal view of a left fifth metacarpal of *Rhamphorhynchus Bucklandi*, in Dr. Wright's Collection.

Fig. 9. Part of the proximal phalanx of a fifth or long finger, in the Rev. Mr. Witt's Collection.

[PLATE 10]

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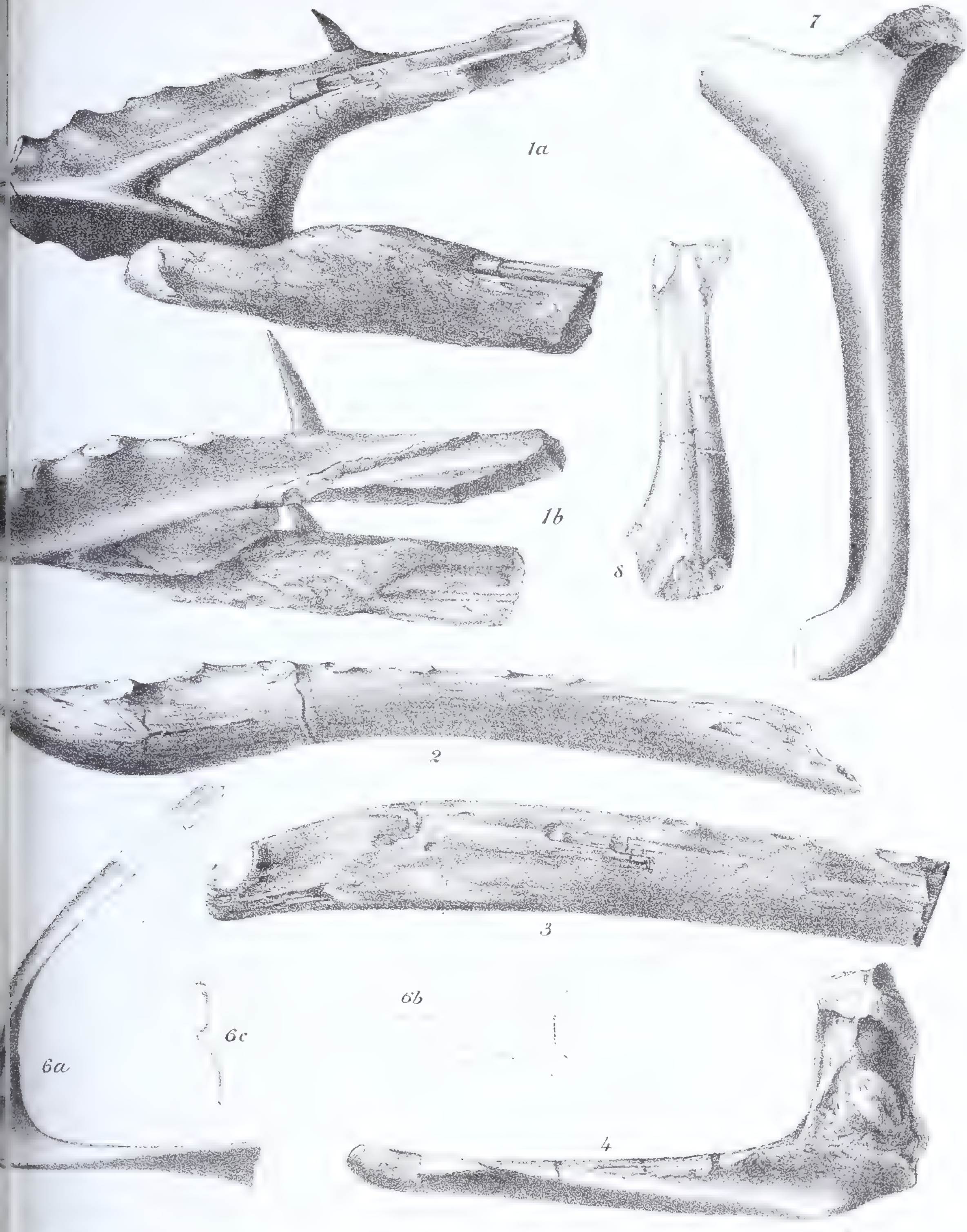

RHAMPHORHYNCHUS

& W del. G West lith.

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IX

ON A FOSSIL BIRD AND A FOSSIL CETACEAN FROM NEW ZEALAND

Quarterly Journal of the Geological Society, vol. xv., 1859, *pp.* 670–677.
(*Read March 23rd*, 1859.)

SOME time ago, my friend Mr. Walter Mantell submitted to my examination two fossil bones from tertiary deposits at Kakaunui and Parimoa in New Zealand.

Of these, the one is the right tarso-metatarsal bone of a Bird belonging to the Penguin family, the other the humerus of a Cetacean of small size.

Fossil Bird.—The former bone (of which a front view is represented in fig. 1, and a back view in fig. 2) measures two inches and a half in extreme length, and rather more than an inch and a quarter across its proximal end. The precise width at the distal end cannot be given, as the innermost part of this extremity of the bone has been broken away; what remains measures $1\frac{1}{16}$th inch.

The proximal end of the bone presents two articular facets,—the one internal, an oval, shallow concavity, looking upwards and a little inwards, the other external, quadrilateral, slightly convex from before backwards, slightly concave from side to side, and inclined more obliquely upwards and outwards. The two facets are separated by a stout median ridge, which rises into a conical tuberosity anteriorly, but dies away posteriorly into a shallow triangular pit. The posterior edges of both facets are rather more raised than the anterior ones; and marked transverse depressions separate both from the upper extremities of the four strong calcaneal ridges which project from the upper part of the posterior face of the bone (fig. 2).

Of these, the innermost is the strongest and longest; and a deep groove divides it from the two middle ones, which are separated by only a very shallow concavity. The outermost ridge prolongs the outer edge of the outer articular facet, with which it is continuous, downwards and inwards, upon the posterior aspect of the tarso-metatarse. Continuing the direction of this ridge, but in addition passing into the outer of the two median ridges, is a strong oblique "linea aspera" which passes downwards and inwards to the proximal end of the broken-off inner division of the distal end of the bone. On the distal side of this ridge, and in the same line with the outer median calcaneal ridge, is the posterior end of an oval foramen about

Fig. 1.—*Front view of the right tarso-metatarse of* Palæeudyptes antarcticus. Nat. size.

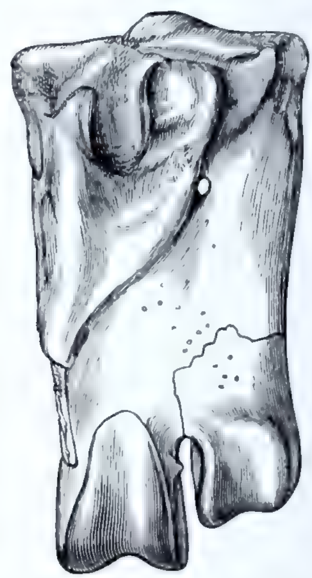


Fig. 2.—*Back view of the same bone* (fig. 1). Nat. size.

$\frac{1}{8}$th of an inch in diameter, which completely traverses the metatarse. Below the ridge, internally, is a shallow, but broad, depression or fossa, which separates it from the middle of the three trochlear condyles into which the distal end of the bone, when entire, was divided.

The anterior face of the bone (fig. 1) presents a very different aspect. Its upper fourth or fifth overhangs the rest, especially on the inner side, where two short parallel ridges are seen running downwards and inwards. The outer and weaker of them ends superiorly in the anterior interarticular tuberosity which was mentioned above. Below it gives off a transverse crest inwards, which subsides before it reaches the inner of the two ridges. On the outer side of, and extending

below this for about $\frac{1}{4}$th of an inch, is a deep narrow pit, which, however, penetrates but a very little way into the substance of the bone. From the inner margins of this pit, three or four thin sharp ridges arise and pass spirally downwards and inwards, the lower ones being much more inclined than the upper; the uppermost ones extend on to the inner surface of the bone, the lower stops short on its front face. Immediately below the interarticular tuberosity the face of the bone is greatly excavated; and this excavation ends below in a very deep groove, which extends through the whole length of the bone, to the fissure which separates the outer and middle condyles. At the superior end of the groove, an oval aperture leads into the canal which terminates in the foramen seen on the posterior face of the bone. The middle part of the groove is deep, but not perforated, while its distal end is shallower. The upper end of the groove is on the same level as the deep pit to which I have previously referred; a somewhat narrow, but strong, bony partition separates the two, and is continued down into the substance of the middle metatarsal bone, which constitutes the inner wall of the groove. Just below the pit and foramen this wall presents an oval roughened space $\frac{1}{4}$th of an inch long, for the insertion of the tendon of the *tibialis anticus*. The outer wall of the groove is more prominent than the inner, and has the form of a strong bony column, which ends above in the outer articular facet; below this, however, it presents a rough transverse ridge, descending lower on the outer than on the inner side, while superiorly and internally it arches over the summit of the groove towards the two inner vertical ridges which have been described.

Its outer and front surfaces exhibit several spiral markings like those on the inner division. Below, this outer column of bone, which is narrow from before backwards ($\frac{5}{16}$ths of an inch), suddenly widens to nearly $\frac{3}{4}$ths of an inch, and presents a semicircular inferior contour when viewed laterally. Its distal end, in fact, is converted into a subcylindrical articular condyle, slightly concave from side to side, and having its anterior and posterior faces oblique to the plane of the bone and to its transverse axis. It is like a portion of a cylinder whose axis is directed upwards, outwards, and backwards, so that its inner edge is more prominent anteriorly, its outer edge posteriorly, and its inner edge inferiorly. A deep broad cleft, corresponding in length with the articular surface, separates this condyle from a second, developed from the middle of the distal end of the bone. This middle condyle is wider than the outer, measuring fully half an inch transversely; it is also deeper, having an antero-posterior diameter of fully $\frac{3}{4}$ths of an inch; and it is longer, for, though its

proximal end is on the same level as that of the outer condyle, its distal end extends a quarter of an inch beyond it.

The transverse excavation of the articular surface is also greater; the articular surface itself extends over $\frac{3}{4}$ths of a circle, and is narrower superiorly than inferiorly; while its inner lip projects a little beyond the outer, in front and above. For the rest, the median plane of the condyle is parallel with the axis of the bone; and its articular surface might be represented by a grooved segment of a cylinder whose axis should be perpendicular to the axis of the whole bone. Of the third or inner condyle, nothing remains but a rough space indicating where it has been broken off. There is an irregularly tuberculate area on the upper part of the inner face of the bone, which perhaps marks the attachment of a rudimentary inner toe.

Those acquainted with the osteology of birds will entertain no doubt that this is the tarso-metatarsal bone of an animal of that class; while the short, stout, proportions of the bone and the deep grooves, pits, and foramina, which indicate the lines of division of the primitively distinct metatarsals, demonstrate that it belonged to one of the squamipennate or Penguin tribe.

Of the Penguins several genera are found in the southern hemisphere, ranging from New Guinea to within the antarctic circle. The proportions of these birds are such, however (the tarso-metatarse being always very short in comparison with the length of the body), that the bone that I have described in all probability belonged to a Penguin of larger dimensions than any living species which have been observed, massive as some of these birds are.

Sir James Ross states that the largest "Emperor Penguin" (*Aptenodytes Forsteri*, Gray, the largest species of the group) caught during his expedition weighed seventy-eight pounds; but he does not give its length. Specimens of some of these birds, obtained during the voyage of the "Erebus" and "Terror," are to be seen in the British Museum; but the largest does not stand 3 feet 6 inches high. The fine skeleton of an Emperor Penguin in the same collection measures, as it is set up, about 2 feet 5 or 6 inches in height; and I do not suppose that the bird to which it belonged could possibly have stood more than three feet high. Now the right tarso-metatarse of this skeleton measures only $1\frac{3}{4}$ inch in length; so that, in this dimension, the fossil is to it as 10 : 7, or nearly half as long again, and its owner might have stood between four and five feet high, supposing that the general proportions of the two animals were alike.

On making a careful comparison of the fossil bone with its homologues in other Penguins, I found that it differed in many respects

from the tarso-metatarse of *Aptenodytes*, which is broader in proportion to its length, is traversed by two distinct interosseous foramina, has a much less-marked external longitudinal groove on its anterior face, and has only two distinct calcaneal ridges, of which the inner arises from the whole width of the upper end of the inner component of the metatarse. Furthermore there is no posterior oblique "linea aspera"; and the surfaces of the bones are altogether smoother. In these respects I find that the skeletons of both of the large Penguins (*A. Forsteri* and *A. Pennantii*) which I have examined agree with one another, and differ from the fossil.

The tarso-metatarse of a smaller member of the same family, the Crested Penguin (*Eudyptes chrysolophus*), much more nearly approximates to the characters of the fossil bone. The tarso-metatarse of *Eudyptes* measures $1\frac{1}{4}$ inch in length by $\frac{5}{8}$ths of an inch wide at its proximal extremity (the same proportions as in the fossil), while the distal end has a width of $\frac{13}{16}$ths of an inch.

There are two interosseous foramina, as in *Aptenodytes*; but the outer is the longer and narrower, and the groove prolonged from it on to the anterior face of the bone is the deeper,—in both which respects *Eudyptes* approaches the fossil and differs from *Aptenodytes*. Again, there are two short oblique ridges on the upper part of the anterior face, above the inner foramen, in *Eudyptes*; and there is a small tuberosity on the inner side of the outer foramen, which, if broken or worn, would give rise to just such an oval rugose area as that I have indicated in the fossil.

On the other hand, the latter differs from the corresponding bone of *Eudyptes* in the division of the calcaneal ridges into four, in the more slender and crest-like form of the inner one, in the cæcal ending of the inner foramen and in the "linea aspera" on the posterior face, and in indicating a bird of twice the size of any *Eudyptes* that I have seen.

I have further compared the tarso-metatarsal bones of *Spheniscus demersa* and *S. minor* in the Museum of the College of Surgeons with the fossil one. Their proportions are like those of *Eudyptes*; they have a tubercle on the outer side of the middle metatarsal bone very like that in the fossil; and in the form of the upper part of the anterior face of the bone in *S. demersa*, is very similar to that exhibited by the bone from New Zealand; but there is a completely open inner interosseous foramen, and the inner and middle metatarsals are separated by a deep, though narrow, groove as long as the outer one. There is the same absence of spiral ridges and of a "linea aspera" as in the *Eudyptes*.

On the whole, therefore, the fossil is less like *Spheniscus* than *Eudyptes*.

In view of the resemblances and differences which I have pointed out, I cannot regard the fossil bone as a part of a Penguin belonging to any known genus; and I therefore propose to institute the new genus *Palæeudyptes* for it. The present species may be termed *P. antarcticus*.

This is not the first time that the remains of the Penguin have been found fossil, Dr. Mantell having briefly alluded to their occurrence in his paper "On the Remains of Birds from New Zealand," published in the Journal of this Society in 1850; but, so far as I know, no particular description of such fossils has hitherto been given.

The bone which I have described was found by a native in the limestone[1] of Kakaunui, and was brought to Mr. Mantell imbedded to some extent in a matrix which was readily recognizable as that particular limestone. Mr. Mantell informs me that the Kakaunui limestone is overlain by a mass of blue clay, that upon the blue clay is superimposed a bed containing freshwater shells, and that upon this, again, lies the alluvium in which the remains of the *Dinornis* are found,—the last, in Mr. Mantell's opinion, having unquestionably coexisted with, and been killed and eaten by man.

The marine shells contained in the blue clay and in the limestone are different from those now living in the seas of New Zealand. It would appear, therefore, that the Kakaunui Limestone is at least of Pliocene age, if not, as Mr. Mantell suspects, much older.

Whatever be the precise age of the fossil, it is not a little remarkable to find in strata of such antiquity the remains of a bird the whole of whose congeners are at present absolutely confined to the Southern Hemisphere, and therefore, in a broad sense, to the same great distributional area. If the strata be of Pliocene age, the fact is in accordance with the relations which have been observed to obtain between the recent and Pliocene faunæ of the Northern Hemisphere. On the other hand, the little that is at present known respecting the distribution of Birds in time is not inconsistent with the ascription of a far greater antiquity to a genus as closely allied as *Palæeudyptes* to those which now exist.

Fossil Cetacean.—The Cetacean bone (figs. 3 and 4) is a left humerus, which was obtained at Parimoa, about five miles north of Kakaunui, from the blue clay above referred to, and is therefore of more recent date than the *Palæeudyptes*. It measures $3\frac{1}{4}$ inches in

[1] See Quart. Journ. Geol. Soc. for August 1850, vol. vi.

total length; $1\frac{1}{2}$ inch in depth, from before backwards, at its distal end; about 2 inches in extreme width at its proximal end. In the middle of its length it measures $1\frac{1}{8}$ inch in width, and $1\frac{3}{8}$ inch in depth. The middle of the shaft is therefore a good deal compressed from side to side; but its preponderating depth arises, in great measure, from a thick protuberant ridge which occupies the two upper thirds of the outer half of its anterior face (fig. 3). Superiorly, this ridge is bounded by a wide transverse groove, which marks the great tuber-

Fig. 3.—*Anterior face of the left humerus of* Phocænopsis Mantellii. Nat. size.

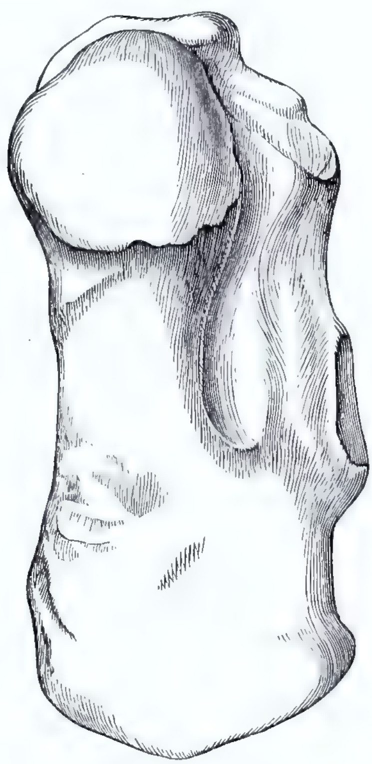


Fig. 4.—*Inner face of the same bone* (fig. 3). Nat. size.

osity of the humerus in front, and is continued downwards upon the inner side of the ridge, terminating, above its inferior end, in a sort of *cul-de-sac*. Inferiorly, the ridge ends in a roughened oval protuberance, which occupies the lower of the two median fourths of the longitudinal diameter of the bone; and, as this tuberosity is abruptly truncated below, the lower fourth of the bone is considerably narrower than its middle part, when viewed laterally.

The posterior face of the humerus is slightly concave, very wide (1·9 inch) above, where it spreads out into the articular head on the inner side and the tuberosity on the outer, but narrowing below to

not more than $\frac{3}{5}$ths of an inch. At this part it is very rough and irregular for a space of $\frac{2}{3}$rds of an inch, forming a facet with which the anterior face of the olecranon was connected. The superior part of the posterior face is excavated by a deep cavity; but I suspect this to be an accident arising from the destruction of the loose, cancellated, bony tissue of this region.

The outer face of the bone is slightly convex from before backwards; concave from above downwards, owing to the great projection of the tuberosity of the humerus outwards.

The inner face (fig. 4) exhibits, above, the articular head, which descends upon it, anteriorly, the deep longitudinal groove to which I have referred above, and posteriorly, opposite the lower end of this, a roughened elevation.

Inferiorly, the inner face is flat; superiorly it is concave, owing to the projection inwards of the articular head. This looks upwards and inwards; it is smooth, convex, and pyriform, the small end being turned outwards and upwards. Its greatest length is $1\frac{1}{3}$ inch, its greatest breadth 1 inch. Externally it is separated by a shallow curved depression from the tuberosity.

The distal end of the bone presents two articular facets for the radius and ulna, which might be represented by two half-ovals united by their straight edges, in a ridge which traverses the distal end transversely, and is nearer its posterior than its anterior end. The anterior or radial facet, in fact, measures $\frac{4}{5}$ths of an inch in length, while the posterior or ulnar does not exceed $\frac{3}{5}$ths. The anterior facet looks downwards and slightly forwards, the posterior downwards and slightly backwards; the latter passes into the olecranar facet, which, looking directly backwards, is of course almost at right angles with the proper ulnar facet.

One of the most remarkable features presented by this bone is its slenderness, the long diameter being to the antero-posterior diameter of the distal end as $2\frac{1}{3}$ to 1.

In *Balæna*, *Balænoptera*, *Delphinus*, *Orca*, and *Hyperoodon*, the antero-posterior diameter of the distal end bears a very much greater proportion to the length of the humerus. Thus, for instance, in a *Delphinus tursio* in the Museum of the College of Surgeons, whose humerus has nearly the same length as that of the fossil, viz. $3\frac{1}{2}$ inches, the antero-posterior diameter of the distal end is $2\frac{1}{2}$ inches, or the two diameters are as $1\frac{2}{5}$ to 1; and the corresponding bones in such species of the other genera mentioned as I have examined have similar or even broader proportions.

In a skeleton of *Monodon monoceros*, between 9 and 10 feet long,

in the same collection, the humerus has a length of $4\frac{3}{4}$ inches, and a distal antero-posterior diameter of $2\frac{1}{4}$ inches; in other words, these diameters are as $2\frac{1}{9}$ to 1,—proportions which much more nearly approximate those of the fossil. But then the radial and ulnar facets are nearly equal: there is no distinct facet for the olecranon; and there is no anterior ridge.

The nearest approximation to the fossil, which I have been able to meet with, is the humerus of the common Porpoise (*Phocæna communis*) of our own seas. Its length is to the antero-posterior diameter of its distal end as about 2 to 1. It exhibits an anterior ridge, bounded by a groove on its inner side; its inner face has a slight elevation on the posterior half of its middle region; the radial facet is larger than the ulnar; and there is a distinct olecranar facet. But the plane of this facet is very little inclined to that of the rest of the ulna; the tuberous part of the anterior ridge occupies the lower third of the anterior face, and is separated by but a very small space from its distal end; and the anterior ridge above it is almost obsolete, so that the bone appears much constricted superiorly.

While it presents certain resemblances to the humerus of *Phocæna* therefore, the fossil bone differs widely from it, and still more from the same bone in any other genus of the *Cetacea* with which I have been able to compare it. I consider it therefore to indicate a distinct genus of *Cetacea*, which may be called *Phocænopsis*, and, after its discoverer, *P. Mantelli.*

X

ON THE DERMAL ARMOUR OF CROCODILUS HASTINGSIÆ

Quarterly Journal of the Geological Society, vol. xv. 1859, *pp.* 678–680.
(*Read March 23rd,* 1859.)

PLATE XXV. [PLATE II.]

A CONSIDERABLE number of Crocodilian scutes, collected by the late Marchioness of Hastings at Hordwell, are now deposited in the Museum of Practical Geology. These scutes may be divided into two great groups—1, *angulated*, and 2, *flat*. The former are distinguished by the angle, open downwards, or towards the ventral side, which their lateral halves make with one another, and by the raising up of their outer surfaces into a more or less prominent longitudinal ridge along the line of angulation. The under surfaces of these scutes are more or less concave from side to side, and convex from before backwards. The flat scutes, on the other hand, are flat, or at most a little convex from side to side above, and slightly concave in the same direction below. There is a singular disproportion between the two kind of scutes, for, out of some hundreds, only two or three incomplete specimens exhibit the peculiarities of the flat scutes.

The angulated scutes (figs. 1–7) may be subdivided into two kinds, those with, and those without, an anterior articular facet, the former being the more numerous.

The *angulated scutes* provided with an *articular facet* are in their general characters so like those which I have described in my paper on *Stagonolepis* (Quarterly Journal of the Geological Society, 1859), that I will only refer to their special characteristics. There are two kinds of them, the one set much, the other very little bent down at

the sides, or, in other words, angulated. The *strongly angulated articulated scutes* (figs. 1 and 2) have the greater part of their posterior margins nearly parallel with the anterior, and one lateral margin is straight and provided with irregular serratures for sutural union with another scute. The other lateral margin, on the contrary, is rounded off into the anterior and posterior margins, and ends in a thin smooth edge, which has evidently lain free in the dermis. The ridge is but little developed in these scutes, and lies over the line of angulation, on the outer side of the median line.

The *slightly angulated articulated scutes* are, when large, broader than they are long (figs. 3, 4, 5). Their four margins are nearly straight, though the posterior may be a little convex backwards, and both lateral margins frequently, but not always, present sutural serrations. The ridge is rather on one side of the middle line, of tolerably equal height throughout, and reaches, but does not project beyond, the posterior margin. Anteriorly, it attains the posterior margin of the groove which separates the articular facet from the rest of the scute.

From these scutes, which attain a width of 2¼ inches and a length of 2 inches, and often have a trapezoidal rather than a rectangular outline, there is a gradual transition down to scutes of an inch in length. With this diminution in size there are perceptible differences in form, the smaller scutes tending to have the figure of longitudinally elongated parallelograms, acquiring proportionally more prominent ridges and having the posterior end of the ridge more produced beyond the posterior margin, which itself becomes more convex (fig. 5).

The angulated scutes without articular facets differ from those first described mainly in the fact of the absence of these facets, but they are in addition, on the average, smaller, coarser, and more irregular (figs. 6 and 7).

The only unquestionable flat scutes I have seen (figs. 8 and 9) are remarkable for the roundness and less regularly radiating arrangement of the pits upon their outer surface. The anterior edge of the scute is straight, thicker than the other, and suturally serrated; of the lateral margins, one is straight and without any definite evidence of sutural notches, the other is rounded off into the posterior margin, which is slightly convex.

I believe that this scute is imperfect, having lost that anterior articular moiety which I have shown (On the Dermal Armour of recent *Crocodilia*: Proc. Linn. Soc. 1859) to be a distinct piece in the ventral scutes of the modern *Caiman* and *Jacare*. In fact, I have

found two examples of this anterior moiety detached, one of which is represented in fig. 8. It exhibits the articular facet, the deep rounded sculpture pits of the other moiety of the flat scute, and the total absence of even the commencement of a ridge, characteristic of the corresponding part of the flat ventral scutes in *Jacare* and *Caiman*, and, finally, its thick posterior edge presents distinct sutural teeth, in relation to which circumstance, I may remark that the scutes break with a smooth, sharp, transverse, fractured surface, totally unlike a sutural edge.

If the two pieces which are figured fitted, instead of belonging, as I suspect they do, to opposite sides of the body, the resemblance of the entire bony plate to one of the ventral scutes of *Jacare* would be most striking.

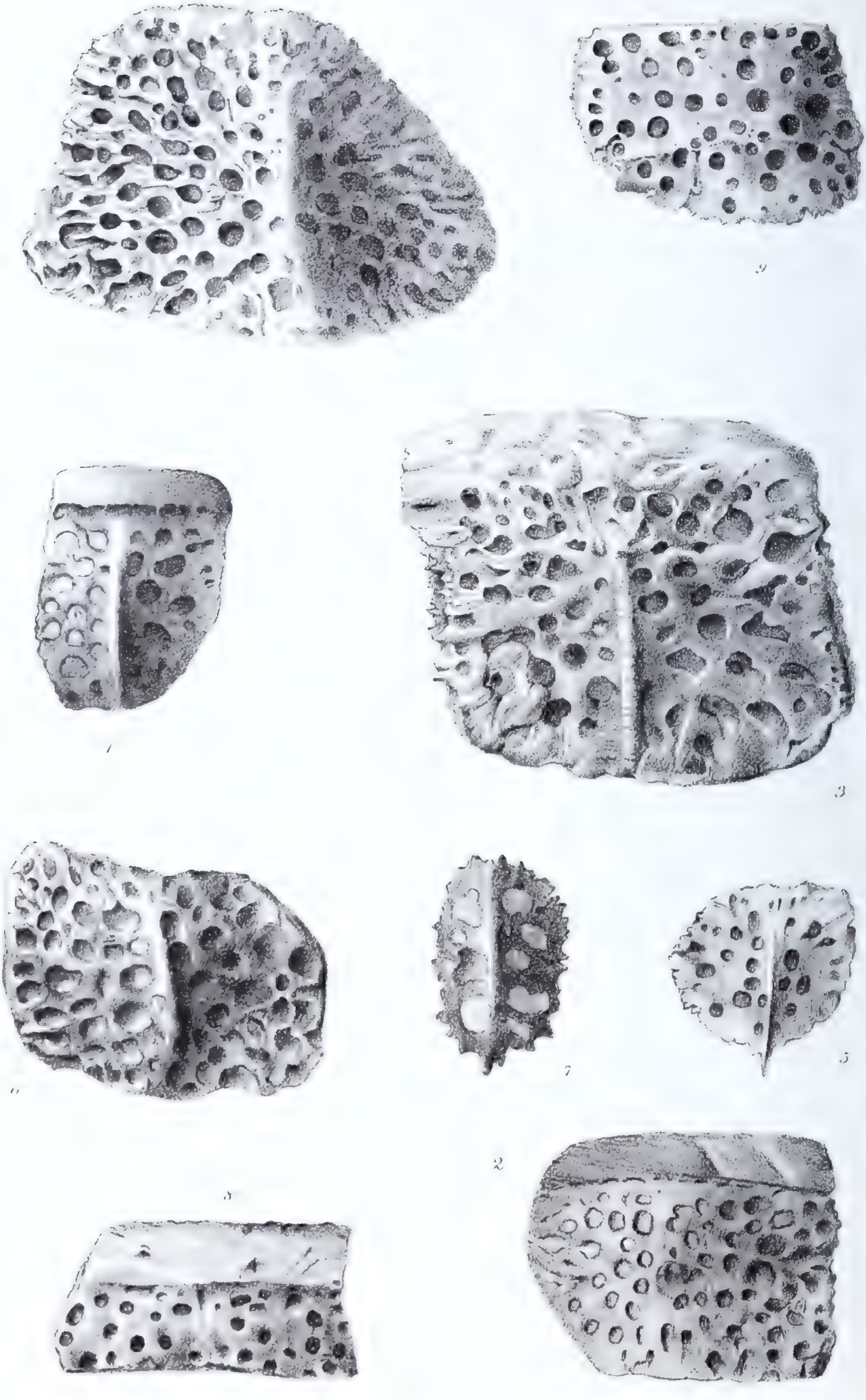
The less angulated articulated scutes again are very similar to the dorsal scutes of *Jacare*, and the more angulated ones to its cervical scutes ; those more angulated scutes, which are devoid of any articular facet, might have occupied the most anterior place in the series of cervical scutes, as such scutes, not being overlapped by others anteriorly, have no facet ; and, finally, the flatter angulated scutes, without articular facets, may very probably have been situated along the extreme outer margin of the dorsal shield.

But, though the positions assigned to these scutes may all be justified by the analogy of the existing *Caiman* or *Jacare*,[1] it is also quite possible that the non-articulated scutes may have belonged to a different species from those which are articulated.

I am strongly inclined, however, to the supposition that all the scutes belong to the same species, *Crocodilus Hastingsiæ*, and that this is the only Hordwell species of Crocodilian Reptile, the so-called *Alligator Hantoniensis* being in fact, as Professor Owen has suggested, only a variety of *Croc. Hastingsiæ*.

In the general form and characters of the skull this Crocodile most nearly approaches the *Crocodilus palustris* or *bombifrons*, one of the two species of true Crocodile which inhabits the Ganges. Now in this Crocodile (as I have pointed out in the 'Proceedings of the Linnean Society' for 1859), the palate not only presents a straight premaxillar maxillary suture (as in the *Alligatoridæ* and in *Croc. Hastingsiæ*), but sometimes one or the other, or even both, canine notches are converted into complete pits, as in Alligators. It would not be surprising, then, to find the same peculiarity occasionally occurring in *Croc. Hastingsiæ*, and still less is it so if we consider the nearer approximation to some *Alligatoridæ* exhibited by the dermal

[1] See my paper on the Dermal Armour of recent *Crocodilia* cited above.



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CROCODILUS HASTINGSIÆ

armour of the last-named Crocodilian. As I have shown, in fact (*loc. cit.*), no true Crocodile or Gavial possesses articulated scutes or ventral scutes.

The teeth are more numerous in Alligators than in true Crocodiles, and, as the dental formula of *C. Hastingsiæ* is $\frac{22-22}{20-20}$, we might regard its dentition as another approximation to the *Alligatoridæ*. But the value of this character is greatly diminished when we reflect that the teeth of Alligators are either equal in number in both jaws, or preponderate in the lower jaw; while the *Croc. Hastingsiæ* retains that preponderance of teeth in the upper jaw which is observed in true Crocodiles and Gavials.

I may remark that a very fine skull of *Crocodilus Hastingsiæ*, for the opportunity of examining which I am indebted to Mr. S. Laing, M.P., F.G.S., coincides in all its characters with the typical specimen of *C. Hastingsiæ* in the British Museum. The roof of the canine pit is, however, somewhat widened.

DESCRIPTION OF PLATE XXV. [PLATE II.]

Figs. 1 and 2. Strongly angulated, carinated, probably cervical, scutes of *Crocodilus Hastingsiæ*.

Fig. 3. A large, slightly angulated, carinated scute from the dorsal region.

Figs. 4 and 5. Smaller, slightly angulated, carinated scutes.

Figs. 6 and 7. Two angulated, carinated scutes, which, unlike the preceding, exhibit no anterior articular facet.

Fig. 8. Anterior moiety of a flat ventral scute.

Fig. 9. Posterior moiety of the same.

All the figures are of the natural size.

XI

BRITISH FOSSILS

Part I.—ON THE ANATOMY AND AFFINITIES OF THE GENUS PTERYGOTUS[1]

Memoirs of the Geological Survey of the United Kingdom, Monograph I., 1859, *pp.* 1–36.

The genus *Pterygotus* was established by Professor Agassiz, in the following note appended to page xix. of his well-known work, the "Monographie des Poissons Fossiles du Vieux Grès Rouge" (1844):—

"The Plate A, accompanying this monograph, represents many well preserved fragments of one of those gigantic Crustacea of the Old Red, collected by Mr. Webster in the neighbourhood of Balruddery, in Scotland. Deceived by the scaly aspect of a portion of the carapace, I at first believed that this might be the type of a peculiar genus of fishes, and to that class I referred *Pterygotus*, in my enumeration of the fossil fishes of the Silurian system, published in Murchison's great work. This genus, founded upon very imperfect fragments from the Ludlow rocks, is now well known, from the investigations which I have been enabled to make of a new species from the Old Red, discovered by Lyell, in Forfarshire, and of which Mr. Webster has found more characteristic remains at Balruddery. The specimens collected by Lyell are those large scutes, of which I have spoken in my 'Recherches,' vol. i. p. 26, and which, in the absence of the means of rigorous determination, have been seriously taken for the remains of superhuman beings.

"Dr. Buckland and I, on examining them carefully, convinced ourselves that they must be the carapaces of Crustacea ; but it was

[1] Part I. of this Monograph is by Professor Huxley. Part II. is by Mr. Salter, and is reproduced here because without it the plates, and much of Professor Huxley's portion of the Memoir, would be unintelligible.—Editors.

only in 1840 that I obtained direct proof that such was the case. In fact, among the specimens collected and communicated to me at that time by Mr. Webster, are fragments of carapaces, segments of the tail, the natatory palettes with which the extremity of the latter was provided, legs, and chelæ. These remains remove all doubt as to the zoological position of the fossil. It is a crustacean of colossal size, having a carapace of more than a foot and a half in width, and a tail about a foot wide. The dimensions of the cephalothorax, represented in the right-hand figure of the second row, Plate A,[1] forbid its arrangement among the *Decapoda*, notwithstanding the form of the chela figured in the middle of the lower series of the same plate.[2] I am rather inclined to believe that this singular animal will become the type of a family, intermediate between the Trilobites and the *Entomostraca*, in which perhaps the *Eurypteri* and the *Eidotheæ* will some day be included. The carapace is ornamented throughout with a squamose sculpture, which confers upon its surface the aspect of a fish's cuirasse; in the middle it presents an impression like that of a lance-head, corresponding, without doubt, to the gastric and cardiac regions of ordinary Crustacea. The divisions of the chela are provided with large obtuse teeth; the longer point of these levers is strongly arcuated. The arm which carried the chela[3] (figured on the left in the lower series) is very large; the articulations which immediately precede the pincer are short, and wider than they are long. The ordinary legs (figured on the left in the middle series[4]) are simple, and end in a point; the segments to which they are attached are sensibly longer than they are wide.

"The segments of the tail[5] (represented in the right-hand figure of the upper series,) reduced to half their natural size, are broad plates, provided with articular processes at their superior extremities. Lastly, the natatory palettes of the tail (the two figures at the superior left-hand and inferior right-hand corners[6]) are rounded plates, fringed along their edges, and scaly on the surface, like the carapace. This curious fossil does not seem to be very rare in the

[1] This is in fact the epistoma.

[2] The part thus figured is one of the antennæ.

[3] The figure here referred to represents a part of the palp of the ectognath, which has nothing to do with the chela.

[4] This is an endognath with its palp; no segment is represented in the figure.

[5] The figure represents one of the most anterior segments of the body.

[6] The part shown in the superior left-hand figure is part of the basal joint of an ectognath. The inferior right-hand figure represents the terminal joint of the palp of the same organ.

Old Red of Scotland. I have conferred upon this species the name of *Pterygotus anglicus*, which at once suggests its origin and the singular view which was once entertained as to its nature."

Although the parts figured by M. Agassiz have, as I have taken occasion to point out in successive notes, in no single case the nature attributed to them, his sagacious indication of the affinities of *Pterygotus* deserves thankful recognition.

The views of Professor Agassiz respecting the affinities of *Pterygotus* are adopted and expressed still more strongly by M. von Eichwald, in his Memoir on the Grauwacke of Livonia and Esthonia.[1] "It appears at first sight," says he, "that this (*Pterygotus*) was a colossal *Eurypterus*, at least the genera are very closely allied." M. von Eichwald differs from Agassiz only in considering the latter's "caudal segment" to have been thoracic. His specimen, which he ascribes to *P. anglicus*, was found in the Limestones of Rootsiküllc.

In the "Annals and Magazine of Natural History" for 1849, series 2, vol. iv. pp. 393, 394, Professor M'Coy gives an account of the remains of a new species of *Pterygotus*, *P. leptocheles*. In his preparatory remarks, Professor M'Coy erroneously states that Agassiz has "in his work on the Fishes of the Old Red Sandstone referred it (*Pterygotus*) to the *Entomostraca*, without indicating any particular division." The fact being, as is proved by the quotation just given, that he does not consider *Pterygotus* to be entomostracan at all, but to be intermediate between "*Trilobites and Entomostraca*."

Following Agassiz and Eichwald, Professor M'Coy indicates the close relations which obtain between *Pterygotus* and *Eurypterus*; but he unites *Pterygotus*, *Eurypterus*, and *Bellinurus*, and makes of them a family of the *Pœcilopoda*. Professor M'Coy considers that he has found evidence of the existence of more than one pair of didactyle feet.

Professor M'Coy's views are further expressed in the restored figures of *Pterygotus*, which he has furnished to the fifth edition of Sir Chas. Lyell's "Manual" (1855), and in the following passage of that work (p. 420):—

"The carapace of this huge crustacean, which must have rivalled, if not exceeded in size, the largest crab, is furnished at its hind part with two short prongs, and has two large eyes near the middle, much like those of the *Eurypterus* found in the coal-formation of Glasgow. The body consists of ten or eleven movable rings (the exact number is not ascertained), and was terminated

[1] Die Grauwacke Schichten von Liv- und Esth-land, von Ed. von Eichwald. Bulletin de la Société Impériale des Naturalistes de Moscou.

by an oval pointed tail. The whole surface is covered by the scale-like markings before mentioned as ornamenting the head. Professor M'Coy, to whom I owe these notes on the general structure, has kindly furnished me with a restoration of the entire animal (fig. 543), which he believes to be closely allied to the great *Eurypterus* before mentioned, if not of the very same genus, and moreover of the same family as the living king crab or *Limulus*."

The restorations exhibit, in figs. 542, 543, 544, the chelæ fitted on to the ends of the mutilated ectognathary palp, in accordance with Agassiz's idea of their position ; while in fig. 543, the epistoma is represented as the carapace, and a transversely elongated eye is made to appear on either side of its median lobe, about midway between the middle line and the margin ! The chelate appendages are made to arise from behind this supposed carapace, and are succeeded by two or three pairs of articulated appendages. In short, wherever Professor M'Coy departs from M. Agassiz's conception of the structure of *Pterygotus*, the alteration is not an improvement.

In 1852 Mr. Salter published a "Description of the *Pterygotus problematicus*," in the "Quarterly Journal of the Geological Society," in which the following passage occurs :—

"It is probable that there are numerous species of the genus in the old rocks. Fragments, with the characteristic markings, occur in Upper Silurian shale at Gaspé, Lower Canada ; and portions of the limbs of a Bohemian species have been figured by the late M. Corda as the feet of *Brontes*, a genus of Trilobites."

Mr. Salter expresses his concurrence in the systematic views of Professor M'Coy.

The Report of the British Association for 1855, "Transactions of the Sections" (pp. 89–91), contains the abstract of a paper by Mr. D. Page, "On the *Pterygotus* and *Pterygotus* Beds of Great Britain." The following passages show what views were then entertained by Mr. Page with respect to the structure of these animals :—

"The *Pterygotus*, of which there appeared to be three distinct species,—the gigantic *problematicus*, the *anglicus*, and the *punctatus*, —was altogether different in its general structure from any crustacean living or extinct. The portions chiefly found (and of these capital specimens are in the collections of Lord Kinnaird, the Watt Institution, Dundee, &c., all originally from Balruddery,) were the frontal cephalic shield, the posterior cephalic or thoracic shield, with its lunar-like epimera, the abdominal segments, generally from

seven to eleven in number, the huge prehensile claws with their curious denticulated edges attached to limbs of great length, the shorter swimming limbs with their paddle-like appendage, and several semi-oval detached plates which evidently belonged to the breast or under side of the animal. Putting all these portions in place as nearly as could be determined, we had a huge lobster-like crustacean, but only lobster-like in general contour, for in its true generic relations it belonged to no existing family of the order. Partly phyllopod and partly pæcilopod, in its abdominal segmentation macrourous, and in its thoracic apparatus resembling the existing *Limulus*. The *Pterygotus* could be classed with no living family, and was in aspect more like the larvæ than the adult forms, of any Crustacea with which we are acquainted. This peculiarity, indeed, ran throughout the whole of the Crustacea (and there were several new forms he would notice on another occasion) which had hitherto been found in this geological horizon,—a horizon that would yet be found to be marked peculiarly by its strange Crustacea. From the portions he now exhibited to the section, the members could perceive at a glance that the restoration by Professor M'Coy was altogether erroneous, and bore scarcely any resemblance to what the creature must have been when alive, and acting the part of a scavenger along the muddy shores of the Old Red Sandstone seas. The figures on the walls (Mr. Page here exhibited what he conceived to be a near approach to a complete restoration) would afford some idea of the general features of the animal, which he had found of all sizes from ten or twelve inches up to full five or six feet in length. Such was the *Pterygotus*, and looking at its complex structure, as well as the similar structure of other Crustacea of the period, there could be no doubt that no existing classification of the order embraced them in its subdivisions. The fact was, that the existing Crustacea were by no means well worked out as a group, and the discovery of these strange fossil forms rendered the study still less perfect."

The comparative anatomist acquainted with the labours of Milne Edwards, Dana, Bell, Baird, Schaeffer, Darwin, and a host of other workers, will hardly be disposed to agree with the opinion expressed in the commencement of Mr. Page's last paragraph, though doubtless a good deal remains to be done. In Mr. Page's reference of the *Pterygoti* to a distinct group, he has, as we have seen, been anticipated, and his restoration of their structure is hardly more fortunate than that of his predecessors. His "posterior cephalic or thoracic shield" is the epistoma, and has a wholly different place from that

assigned to it; like Agassiz and M'Coy he places the chelæ at the end of the ectognathary palps, and considers them to terminate thoracic appendages.

Mr. Page's paper was read before the British Association at its meeting in 1855. In November of the same year Mr. Salter communicated a paper to the Geological Society "On some new Crustacea from the Uppermost Silurian Rocks," to which I added a note on the structure and affinities of *Himantopterus*.

Mr. Salter points out the differences between *Himantopterus* and *Eurypterus*, and establishes six species of the former genus, whose structure and affinities are discussed in my own note. Subsequent investigation has confirmed the views therein taken of the carapace, its eyes, the chelate antennæ, the swimming feet, the general structure of the body, and the absence of abdominal or thoracic appendages; nor has it, as yet, been absolutely proved that there were more than three pairs of cephalic appendages; but the basal joints of the ectognaths were mistaken for mandibles, and their connexion with the long palp-like swimming foot was not observed. Neither the epistoma nor the metastoma (the latter is figured in the restoration as a "scale-like appendage") were determined. In inquiring into the affinities of *Himantopterus*, I compared it successively with the *Phyllopoda*, the *Pœcilopoda*, the *Copepoda*, and the grounds on which I objected to refer it to either of these orders seem to me still, substantially, to hold good. I then proceeded to compare it with the Cumoid *Crustacea*, with certain *Stomapoda*, and with the embryonic forms of the higher *Crustacea*, and I concluded by expressing the opinion, that "the nearest approach to *Himantopterus* which could be constructed out of the elements afforded by existing *Crustacea*, would be produced by superinducing upon the general form of a Cumoid crustacean, such a modification of the appendages as we find among the Zoœiform Macruran larvæ."[1]

In his "Advanced Text-Book of Geology," p. 135 (1856), Mr. Page gives a figure of one of the specimens on which *Himantopterus* was based, and provisionally admits that genus, adopting the "Cumoid" affinities which I had suggested. He considers that those palæozoic Crustacea and their allies exhibit, "as it were, an interfusion of phyllopod, pæcilopod, and decapod—of brachyurous, macrourous, and xiphosurous forms," and figures and names "*Sli-*

[1] Mr. Salter has misunderstood me, when he says at the end of his memoir (*l.c.*) that I consider *Himantopterus* to be "one of the *Stomapoda*." On the contrary, I have always been prepared to admit the ordinal distinctness of the *Eurypterida*.

monia" and "*Stylonurus*," which he considers to be new genera, but which are not as yet proved to be other than species of *Eurypterus* and *Pterygotus*.

Mr. Salter communicated to the meeting of the British Association, in 1856, a paper "On the great *Pterygotus* (seraphim) of Scotland, and other Species," containing his opinion as to the identity of the genera *Himantopterus*[1] and *Pterygotus*, and some of the further anatomical facts which had at that time been elucidated.

And, lastly, I stated the results of the same inquiries still more fully in my "Lectures on General Natural History," published in the "Medical Times and Gazette" for 1857.

The evidence upon which the following attempt to give a connected account of the structure of *Pterygotus* is based, is both positive and negative. Numerous specimens testify to the existence of certain characteristically formed parts, and to the arrangement of these in a definite order in the body of the animal, so that its general configuration may be very confidently restored. On the other hand, the large number of fragments of many species of *Pterygotus* which have been inspected, without revealing anything new, leads me to entertain a strong impression that no structures of any very great importance remain to be discovered.

With regard to the nature of the positive evidence, I may premise that of the fifteen distinguishable species of the genus, the remains of only five, viz., *anglicus*, *acuminatus*, *punctatus*, *perornatus*, and *bilobus* have yielded facts of capital importance in a structural point of view; I shall, therefore, confine myself to these species, referring the reader to the systematic portion of this monograph for information respecting the rest, and indeed for all details of no anatomical importance concerning even these.

Of the species named, the only entire specimens yet discovered belong to *P. bilobus*, but the large size and comparatively perfect condition of the detached parts of *P. anglicus*, added to the fact that the genus was originally founded on this species, render it convenient to commence with a description of them.

1. *The Carapace.*—In Lord Kinnaird's collection there is a large flattened plate, figured in Plate III. [Plate 14] fig. 1, which appears to have possessed a trapezoidal form when perfect, but is at present very irregular (though by no means distorted), one of its angles and a considerable portion of the margin of the longest side having been

[1] The name *Himantopterus* could in no case have been retained, as it has been already used for a genus of lepidopterous insects.

broken away. The shortest or anterior side is very slightly convex, the opposite and parallel longest side is a little concave ; that lateral margin which is entire is nearly straight, but is rounded off where it joins the posterior edge. The surface of the fossil is slightly concave, and exhibits neither sculpture nor distinct granulation, but it is marked by a great number of sinuous elevations and depressions. At the outer extremities of the anterior edge are two large and deep depressions of an oval form, having their long axes directed obliquely forwards and inwards.

The surface of each concavity presents a great number of minute, but regular and close-set depressions (Figs. 1 *a*, 1 *b*), which appear quite distinct when viewed from a little distance, but whose form is by no means easily defined on closer inspection. On the inner side of one of these concavities a broad longitudinal depression traverses the surface for some distance. *Primâ facie*, one would be inclined to take this great plate for a carapace, and the lateral, peculiarly sculptured, concavities for the vestiges of eyes ; and any doubt on the subject will be at once removed on comparing it with the carapaces of *Pterygotus bilobus* or *perornatus* (Plate I. [Plate 12] figs. 1, 13) ; but it is somewhat difficult to decide whether the fossil is merely the impression of the dorsal surface of a carapace, or whether we really see the inner face of the carapace itself. The absence of the characteristic sculpture is not conclusive against the former determination, as, with the exception of its anterior edge, the dorsal surface of the carapace of *P. perornatus* is equally devoid of ornament.

However this may be, the long margin must clearly be posterior, and the entire lateral edge, the right, while the piece broken off is the left posterior lateral angle. If a line be drawn so as to continue the direction of the anterior part of the left edge backwards until it meets the line of the posterior edge, it will represent the general course of the broken margin, and the carapace will then be found to have had a trapezoidal form, the posterior edge being nearly twice as long as the anterior, and the antero-posterior diameter being about equal to the length of the anterior margin. The right lateral edge is more or less crushed and distorted.

This is the only known example[1] of the carapace of *P. anglicus;* the fossil described as such by Professor Agassiz must therefore have a totally different nature.

2. *The Epistoma.*—It is this remarkable structure which is

[1] Mr. Salter informs me that there are two more in Lord Kinnaird's collection, which I have not seen.

figured in a state of greater or less perfection in Plate III. [Plate 14] figs. 2, 7.

The most perfect specimens (figs. 2, 5,) reveal a broad plate having one edge nearly straight, but presenting a slight median emargination, while the opposite edge inclines from the middle line on each side outwards towards the straight margin, which it would, if continued, cut at a considerable angle.

In the middle line a slight longitudinal depression passes along the face of the plate for a short distance, from the straight margin towards the convex one, and then divides into two diverging grooves.

From the extremities of these, two others, slightly convex towards one another and the median line, are continued as far as the convex edge, and thus the plate becomes divided into three regions,—a narrow " median lobe " and two wide " lateral alæ." The inner angles of the alæ are rounded off; the median lobe projects beyond them and ends in a sharply defined, well-rounded, free edge. The outer fourth of the transverse diameter of the median lobe on each side is overlapped by the corresponding ala, a considerable amount of matrix being occasionally interposed between the two. The general plane of the median lobe, in fact, lies behind that of the alæ, whence it arises that impressions of the plate present the aspect figured by M. Agassiz, and reproduced in Plate III. [Plate 14] fig. 2, and the median lobe, while covered by the alæ, appears spoon-shaped, whereas its end is in reality but little expanded (fig. 7).

The alæ present, very well developed, the peculiar sculpture so characteristic of *Pterygotus* and its allies, multitudes of little semi-lunar facets, with their convex edges raised and all turned towards the convex margins of the plate, being thickly scattered over its surface.

The facets of the sculpture on the middle of the median lobe are greatly elongated, but have the same general direction. The rounded end of the median lobe is marked by radiating striæ, while its sides, where overlapped by the alæ, are smooth. From the thinness and sharp definition of its edge, the median process would seem to have been quite unconnected with the alæ laterally; and it appears to have very readily yielded to force along the diverging grooves. The impressions of median lobes detached, in consequence of having broken away from the alæ along these lines, are figured in Plate III. [Plate 14] figs. 3, 4.

No crustacean, living or extinct, is known to have a carapace

presenting the least approximation to the structure here described, and the true carapace of *Pterygotus* has already been described. I shall endeavour to prove by and by that this singular plate is in fact the homologue of the epistoma and labrum of other *Crustacea*.

3. *The Body Segments.*—Numerous oblong plates and impressions of such, ornamented more or less extensively with the peculiar sculpture, have been discovered (Plates IV. and V.) [Plates 15, 16]. Of these, some are much elongated transversely, and, if we may be guided by the analogy of *P. bilobus* and *perornatus*, belonged to the anterior part of the body. Others are longer than they are broad, and it may be concluded, on similar grounds, that they represent posterior segments. In the specimen figured in Plate IV. [Plate 15] fig. 6, two such segments remain in their natural relation to one another, but it is, unfortunately, impossible to ascertain whether they simply overlapped one another and were merely connected by membrane, or whether their union was effected by a more definite articulation. In Plate IV. [Plate 15] fig. 1, a segment is seen to send a strong process forward from its anterior and external angle, and a similar structure appears to have obtained in the specimen figured by Professor Agassiz, in the right-hand upper corner of his Plate A (*loc. cit.*). This process may have served to articulate the segment with its predecessor, or it may have given attachment to muscles.

The specimen figured in Plate V. [Plate 16] fig. 2, would at first appear to indicate that the segment had a sub-circular or elliptical section, but it is so much crushed and distorted, that I am not inclined to lay any great stress upon the conclusions which may be drawn from it, the more especially as all the other specimens which give a view of the thickness of the body rather lead to the belief that it was considerably depressed, at any rate, posteriorly. The segment, probably penultimate, figured in Plate V. [Plate 16] fig. 3, for example, exhibits no signs of having undergone any very considerable compression, and yet its thickness does not equal more than one-fourth of its breadth. It is quite possible, and indeed probable, however, that the proportions of the antero-posterior and transverse diameters may have been different in the anterior and posterior segments.

It is probable that the segments were sculptured on the ventral, as well as on the dorsal surface, in all cases, as that last referred to certainly is so. No segment has as yet exhibited any trace of an appendage or of an articular surface for one.

A specimen in the possession of Mr. Lightbody exhibits at least

eight segments connected together, but there is no evidence as to the total number composing the body of *P. anglicus.*

4. *The Telson.*—Reasoning from the analogy of *P. acuminatus*, &c., the part figured in Plate V. [Plate 16] fig. 6, must be the telson, or terminal segment of the body, of *P. anglicus.* It is particularly described in the systematic portion of this Monograph (p. 233). I will merely remark, therefore, that it is oval, truncated anteriorly, mucronate posteriorly, and serrated along the lateral edges. It presents traces of a median ridge, and appears to have been very flat.

5. *The Paired Appendages.*—The remains of three distinct kinds of paired limbs, besides single appendages, have been discovered in the same beds with the carapace and body segments of *P. anglicus.* These are :—

(*a.*) The chelate organs figured in the most perfect state in which they have yet been discovered in Plate VI. [Plate 17] figs. 4, 5. Three joints at least may be observed in this member. The first is an elongated subcylindrical stem, flattened by pressure. The next, short, enlarged, and swollen, is produced into a long slender process, pointed and incurved at its extremity, and beset with very strong and numerous, unequal, striated teeth. The third joint is articulated with the enlarged basal part of the second, so that its similarly incurved extremity is opposable, like a thumb, to the latter. It possesses teeth of a similar structure to those in the other ramus of the chela, and opposed to them as the canine teeth in the upper jaw of a mammal are opposed to those in the lower, passing, that is, behind the others, or on their proximal side.

(*b.*) The second kind of appendage (Plate VII. [Plate 18] figs. 4, 5, 6, 7,) presents a large flattened basal joint, produced at one extremity, and truncated obliquely to its long axis at the other. The truncated margin is slightly curved, and is beset with long and strong, curved and pointed teeth, which are longer at one end of the series than at the other ; and are so constricted at their bases as to appear to be articulated with the basal joint.

Of the two longest margins of the latter, the one has a general convexity, while the other is concave. The outer part of the former exhibits a sort of notch or step, in which is lodged the basal joint of a long palpiform appendage. This joint (*c*) is very short and somewhat swollen.

The next articulation (*d*), longer and subcylindrical, is broader distally than proximally. The third (*e*), twice as long as the last, has a nearly equal breadth throughout. It is exhibited *in situ*, and in

its whole length, by only one specimen (Plate VII. [Plate 18] fig. 4), and here the distal extremity is rounded and slightly emarginate.

In the same specimen (and only in this) a fourth joint (*f*) may be observed. It is as long as the third, but of a different form, the distal end being much wider than the rod-like proximal extremity. The internal edge of the distal extremity is rounded and slightly serrated, and is apparently the natural edge of the part; but there are appearances which lead one to suspect that the continuation of the outer angle has been broken away.

The characteristic sculpture is visible upon the surface of the basal joint of this appendage, more particularly towards the anterior edge of its inner region, and the convexities of the facets are here directed towards the convex long margin. The outer wall of its outer region in fig. 4 is broken away, and the matrix contained in the interior has become detached, so as to show the inner surface of the opposite wall, which is perfectly smooth.

In the recent state a considerable interval, doubtless filled by muscular and tendinous soft parts, must have existed between the two walls, as, even in the compressed fossil, the thickness of the matrix filling the cavity sometimes amounts to one-sixteenth of an inch. The third and fourth joints also had a considerable thickness.

(*c*.) Of the third kind of paired appendages the most complete specimens are those figured in Plate VI. [Plate 17] fig. 1, and Plate VII. [Plate 18] figs. 1, 2. It consists of an exceedingly large and expanded, quadrate, basal joint, produced at one angle into a broad curved process, which is obliquely truncated at its extremity. The truncated edge is nearly straight, and is serrated, broad notches separating a number of strong flattened pointed denticles, which are continuous with the substance of the joint, and not articulated with it.

The denticles or serrations form a single series, and diminish in size from one end of the series to the other. The smallest is succeeded by the rounded corner in which the truncated edge and the concave margin of the serrated process meet.

The surface of the joint, and of its process, is covered with the squamiform ornamentation, and presents in the middle of the margin, opposite to the serrated process, a deep notch, which receives the first joint of the long palpiform remainder of the appendage.

The form of these joints is particularly described below (p. 236). I will only remark here that there are six of them, and that the penultimate, much larger than any of the others, is elongated, broad, flattened, and widely emarginate at its distal extremity, where it

articulates with an oval palette-like plate, with serrated edges. A brief comparison of the figures will satisfy the reader that this is the part represented by Professor Agassiz in the lower right-hand corner of Plate A (*loc. cit.*).

From the form of the articulating edges of the joints of the palpiform part of this appendage, I am inclined to think that, as in the chela of the lobster, the plane of motion of each joint formed a considerable angle with that of its predecessor and successor, the result of which would be a sort of feathering, or screw-propeller motion, of the ultimate and penultimate joints during flexion of the limb.

The Metastoma.—The last kind of appendage (Plate VI. [Plate 17] fig. 7 I have to describe is perfectly symmetrical, and hence, even if there were no other means of determining its real nature, its single or azygos character might be divined

It is an oval plate with margins much thinner than the centre, and presenting a median notch at one extremity. It is richly sculptured, the facets having their convexities turned towards the rounded entire end; and it is worthy of notice that the facets are singularly close set around the apex of the emargination. It is as if the plate had been once completely oval and evenly ornamented and had then been folded in at the emargination.

The part represented in Plate VII. [Plate 18] fig. 7, closely resembles the basal joint of the appendage described under the head (*b*) in general aspect, but differs from it in the excavation of the more convex margin, in the length of the latter, and in the fact that the longest tooth arises considerably behind the junction of the curved with the truncated margin. If these appearances do not arise from mutilation or other alteration, this part is probably a fourth paired appendage.

The carapace of *Pterygotus anglicus* has not been found in connexion with the body, nor the epistoma with the carapace, nor any of the appendages with any other part of the body. A peculiar value consequently attaches to those entire specimens of a crustacean formerly denominated *Himantopterus*, but which the further information yielded by the extensive materials on which this Monograph is based, shows to be of doubtful generic distinctness from *Pterygotus.*

A well-preserved specimen of *P.* (*Himantopterus*) *bilobus* is represented in Plate I. [Plate 12] fig. 1. It presents an elongated body, rounded anteriorly and posteriorly, and much narrower in its posterior, than in its two anterior, thirds. Assuming that the dorsal

surface of the animal is exhibited, there lie, on its right side, the remains of two appendages, the anterior disposed so that its long axis crosses that of the body nearly at right angles, and passing by its inner extremity into the middle of the anterior margin of the head; the posterior, lying more nearly parallel with the axis, and traceable forwards, only so far as the posterior margin of the anterior segment or carapace.

The latter has a nearly semicircular outline, but is more produced than a true semicircle would be. On the right side the margin is interrupted by a much elongated oval depression, having its long axis directed forwards and inwards. This is the impression of the eye, and in some specimens it shows a sculpture very similar to that seen upon the eye of *P. anglicus*.

The carapace is succeeded by a number of segments, of which the best preserved specimens exhibit twelve. The anterior ones are transversely, the posterior longitudinally, elongated, and the hindermost, or telson, is oval and deeply emarginate posteriorly. In front of the head, in the specimen figured in Plate I. [Plate 12] fig. 1, and apparently connected with its anterior boundary, lies a semicircular plate with its convex edge turned forwards (*a*). The plate is as broad as the head, but not quite half so long, and its longitudinal axis is oblique to that of the body. In the middle line, it presents a flattened area, bounded by a longitudinal ridge on each side, and rounded off in front. Although the structure of this part is somewhat obscure, I have little doubt that it corresponds with the epistoma of *P. anglicus*, and that it has been thrust out of place and thrown forward.

To the right-hand side of the carapace, opposite the anterior half of the eye, two curved, serrated, linear impressions, convex inwards, appear (fig. 1*a*). The anterior and inner of these is not more than half the length of the posterior and outer, and cuts the latter about its middle. I find no corresponding impressions upon the left side. When the impressions are viewed very carefully with a magnifying glass, in a good light, they present minute but important differences. The serrations of the short impression are concave and striated, and constricted at their bases. Those of the long impression, on the other hand, are flattened and not constricted, and their series is terminated, posteriorly, by a rounded lobe which forms the posterior angle of a broad process whose boundaries become lost externally. Sufficient, however, remains to show the correspondence between this part and the serrated process of the appendage (*c*) of *P. anglicus*, while the teeth of the inner and shorter line are strikingly similar to

those which beset the edge of the basal joint of the appendage (*b*) in that species.

That the impressions in question are in fact the remains of appendages similar to (*b*) and (*c*) becomes a matter of certainty when we examine such specimens as those figured on Plate I. [Plate 12] figs. 3, 4, 8, 9.

In fig. 8 is represented an organ, certainly belonging to *P. bilobus*, whose basal articulation has as nearly as possible the same form as that of the appendage (*c*), and presents, along its free edge, the same continuous serration and posterior rounded lobe. The like resemblance is traceable in the joints of the palp-like appendage, except that in this specimen a structure was observable, not visible in any other, whether of the same or of different species. This is a long taper filament, nearly as long as the ultimate and penultimate joints, lying on their surface, and apparently attached by its thicker end to the distal extremity of the antepenultimate articulation. There are indications that this filament was itself jointed. In figs. 3, 4, 9, the whole appendage, or at any rate its basal joint, is seen *in situ*, and on comparing the serrated edge of any of these with the outer linear impression first described, the source of the latter will be obvious.

The base of this great limb is attached to the hinder part of the carapace; it therefore, without doubt, lay behind the mouth, and as it is the outermost pair of buccal appendages, it will be useful to call it the "ectognath," a term more convenient than "maxilla," "maxillipede," or "swimming-foot," as it involves neither a morphological nor a physiological hypothesis.

The organ which caused the shorter linear impression, lying internal to and in front of, that of the cutting edge of the ectognath is, I doubt not, similar to that which lies detached in two specimens, and is figured in the wood-cut, p. 207. It is unfortunately impossible in either of these examples to trace, as distinctly as might be wished, the precise form of this appendage, but enough is visible to satisfy me that this species was provided with one, if not two, organs on each side similar in general structure to the appendage (*b*) of *P. anglicus*, and quite competent to produce the impression in question.

From its general character I entertain very little doubt that the appendage *b* is the homologue of the mandible of other Crustacea, but as there is some reason to suspect the existence of a third buccal appendage, and as it is impossible as yet, supposing this third jaw to exist, to say whether any given appendage similar to *b*, was first

or second in order, it will be better to term an oral limb in front of the ectognath, an "endognath." The specific name of "mandible" must be assigned to whichever of these endognaths further research proves to be anterior.

The position and general nature of two of the three pairs of appendages of *Pterygotus* having thus been determined, the third presents no difficulty. In the specimens of *P. bilobus*, represented in Plate I. [Plate 12] figs. 1, 3, indeed, the pair of long anterior appendages are so much distorted and damaged that their structure cannot be satisfactorily made out. There is abundant evidence, however, to show that they were similar to the detached chelæ figured in Plate I. [Plate 12] fig. 6, and these are obviously identical with the pincer-like appendage (*a*) of *P. anglicus*.

The epistoma has already been recognised in the plate lying in front of the head, in Plate I. [Plate 12] fig. 1; it remains only to discover the representative of the metastoma, and the position which it occupied in the organism. The form and sculpture of the part represented in Plate I. [Plate 12] figs. 10, 10 *a*, testify that it answers to the organ sought, and a careful examination of most well preserved carapaces of *P. bilobus*, shows a corresponding plate, or its impression, *in situ*. When undisturbed, in fact, the metastoma occupies the middle of the under surface of the carapace, the cutting edges of the basal joints of the gnathites overlapping, or being overlapped by, its lateral margins, and its emarginated extremity being turned towards the anterior end of the head, which it nearly reaches. The posterior rounded margin is in contact with the posterior boundary of the carapace.

A part, having this form and occupying this position, might be regarded as a labrum or as a metastoma. My reasons for giving it the latter appellation are the following:—It may be regarded as pretty certain that in *Pterygotus*, as in other *Crustacea*, a sculptured surface was free and uncovered by other parts, in which case the plate could not have been attached to the inner surface of the epistoma by its sculptured anterior and outer surface; nor, for the same reason, could it have been attached by its inner surface to the sculptured outer surface of the epistoma. The anterior margin of the plate reaches so far forwards that it could not have been attached by that margin to the posterior margin of the epistoma; and, furthermore, when the latter is detached or thrown out of place the metastoma is never found connected with it, but, as in fig. 1, Plate I. [Plate 12], remains in its own proper position.

I have little doubt, therefore, that this plate was attached by its

posterior extremity to the under surface of the hinder half of the carapace; that it lay behind the mouth, and had all the relations of a metastoma, and it will be seen by and by that certain existing *Copepoda* possess a metastoma very like it, except in its very great proportional size.

Putting together the different facts furnished by the remains of the two species of *Pterygotus*, which have been described, it results,—

1. That the body in this genus was composed of a number of segments, which might be thirteen in number.

2. That these segments exhibit a peculiar ornamentation.

3. That the terminal segment, or telson, is liable to considerable specific variation.

4. That the anterior segment is larger than the rest, and forms a carapace, on whose antero-lateral margin two large oval convex eyes are seated.[1]

5. That, attached to the under surface of the carapace, there are eight (or ten) distinct organs, two single and median, and three or four pairs.

6. The former are, in front, the great epistoma; behind, the metastoma; between these lay the oral aperture.

7. The latter are, anteriorly, the chelate organs (antenuæ); posteriorly, the ectognaths, immediately in front of which lay one or two pairs of endognaths.

8. That there is no good evidence of the existence of any other appendages.

Almost all the remains certainly assignable to *Pterygotus*, which have passed through my hands, are easily referable to one or other of the classes of organs mentioned above, and exhibit no anatomical peculiarities worthy of comment, but a few specimens present difficulties to whose discussion I will now proceed.

1. *Pterygotus punctatus.*—The only representative of the endognaths of this species which I have examined (Plate XI. [Plate 22] fig. 5) exhibits a structure somewhat different from that of the perfect endognath of *P. bilobus* and *anglicus*. The anterior and internal angle is rounded off; the series of teeth commencing behind, and not at the anterior extremity of, the inner edge. The straight inner portion of the anterior margin is spinose, and forms a considerable angle with the outer portion, which bears the palp.

[1] Notwithstanding the peculiar character of the markings upon the corneal surfaces of these eyes, I wait for better evidence than I have hitherto met with, before deciding that they were really compound, and that these markings indicate corneal facets.

The latter is four-jointed, the proximal articulation being large, quadrate and setose along its anterior margin, and provided with a large and strong curved spine towards the outer extremity of that margin. The next joint is elongated and curved, its posterior margin being slightly convex, the anterior similarly concave, and towards the distal extremity bearing a curved spine, like that in the preceding joint.

The third joint and the fourth are much shorter. The former carries a spine on its anterior edge. The latter has two spines, one anterior and one terminal. Is this the homologue of that endognath of *Pterygotus anglicus* represented in Plate VII. [Plate 18] fig. 4, or does it, as the structure of its basal joint would seem to indicate, correspond with the apparently different part shown in fig. 7?

2. *Pterygotus acuminatus.*—On the same slab with a large portion of the body and one of the ectognaths of this species, is seen the remains of an appendage whose basal joint clearly resembles the corresponding part in *P. anglicus* (Plate XIII. [Plate 24] figs. 2, 3). It consists of a broad, flattened, quadrate plate, having a series of curved and striated teeth articulated with its well-defined, nearly straight edge. These teeth, however, do not form one even series, either as regards their size or their position. They commence large, near to what I will term the anterior margin of the plate, but not close to it, the antero-lateral angle being rounded off and giving rise to no tooth. In this respect it represents the corresponding part of the endognath of *P. punctatus* just described. After four or five large ones, the teeth rapidly diminish in size and become indistinguishable. The free edge of the plate then makes a slight curve, so that it projects beyond its former line and then gives rise to two teeth of the same size as the most anterior ones, after which it becomes lost beneath the matrix. A depression runs from the commencement of this projecting edge into the crushed and transversely folded, middle part of the plate. In front of this crushed portion, the anterior region of the plate is, in its outer half, richly sculptured; behind and internally, the substance of the organ is for the most part broken away, but shows the remains of a similar sculpture outside the broken edge. The opposite half of the specimen exhibits the impression of the sculpture over this broken part, but in neither half can the ornamentation be satisfactorily traced continuously over the middle crushed region.

The outer part of the joint, just described, is continued into a broad mass, so divided into two portions externally, as to appear like two palps. Each palp-like division appears to possess at least

three joints, and the distal margins of the outer of these joints in the anterior "palp" are produced into strong curved processes or setæ.

The part represented in Plate XIII. [Plate 24] fig. 4, apparently consists of these palpiform appendages detached from their basal joint. Four or five gradually tapering joints are here distinguishable, and each is produced into setæ along its distal edges, while the terminal articulation resembles a curved claw.

The same kind of basal plate, apparently provided with similar appendages, is shown in another specimen (Plate XIII. [Plate 24] fig. 3), but the parts are here overlapped by the broken ectognath, and are so crushed and confused that I can arrive at no satisfactory conclusion regarding them.

A valuable example of *P. acuminatus* from Lesmahago (Plate XV. [Plate 26] fig. 1), although greatly crushed, and at first sight very unpromising, yields a great deal of valuable information on patient investigation, and shows, among other things, that the organs under discussion belong to the mouth and to the endognathary series. In fact, in both halves of this specimen, the ectognath and the metastoma are very clearly traceable, and are evidently almost undisturbed. The palps of the ectognaths are displayed *in situ* on each side; the cutting edges of these appendages are seen on each side of the middle line and are turned towards one another, while the large metastoma lies between them, overlapping their respective inner margins. Internally to their serrated edges, a series of articulated teeth (c'), like those connected with the free edge of the basal joint of the organ described above, can be seen upon each side, but the rest of the basal joint cannot be made out.

On the left-hand side of the head, however, the remains of two palpiform bodies (c), evidently of the same nature as those described above, and provided with similar strong curved setæ, are visible. On the right side is an impression of a similar character, but its minutiæ cannot be satisfactorily deciphered.

The facts I have detailed may be variously interpreted. Either the two palps belong to one basal joint, or there are two basal joints, each with a palp. In the former case there would be one endognath on each side, with a double palp; in the latter, two endognaths, each with a single palp. As the evidence stands at present, I see no means of arriving at a well-grounded opinion on this subject, and I prefer to abstain from conjecture.

3. *Pterygotus perornatus.*—The opposite impressions of part of an example of this species are exhibited by two slabs, each of which

shows more or less distinctly the carapace and one of the body segments.

On the larger slab (Plate XV. [Plate 26] fig. 2), the impression of the metastoma is distinguishable within the outline of the carapace, but it is thrown out of place, so that its long axis is directed obliquely forwards and to the right side, at an angle of forty-five degrees to that of the body. Close to the anterior extremity of the metastoma, but projecting beyond the boundary of the carapace, lies the basal joint (*c*) of an appendage with articulated, curved, pointed and striated, teeth, like those of the endognaths of the preceding species.

The dentated edge of this organ lies almost parallel with the long axis of the metastoma; but beyond it, and more towards the middle line of the body, there is another curved edge (*c*′), similarly provided with striated and articulated teeth, but cutting the first at a large angle. Is this part of a second endognath of the same side, or is it that of the other side turned round? In any case the parts are thrown far out of their natural position.

On the left-hand side, between the base of the metastoma and the middle of the lateral margin of the carapace, the imperfect impression of part of the toothed edge of another appendage (*c*″) is discernible. It is turned backwards (so that it is certainly displaced), and the teeth are somewhat curved and striated. If there are two endognaths on each side, this might well be one of the left pair turned round.

On the left-hand side, the palp (*e*) of the ectognath is in position, but nothing is to be seen of its basal joint. On the right-hand side, the large basal joint of an ectognath lies detached and turned round, so as to have its cutting edge directed backwards. A confused mass occupies the place of its palp.

Where the antennæ should be there is, on the left side, a long and broad dark impression (*b*) fading away externally. On the right side there is a somewhat similar marking which continues the line of that on the left hand, but is very broken and irregular. However, it divides distally into two branches, on the opposed edges of which the remains of the characteristic antennary teeth can readily be discovered (*b*′).

Whether these impressions represent one antenna, or portions of both, I cannot say, but between them, and in front of them, a dark sculptured area (*f*) presents itself, which is cut off anteriorly by the fractured edge of the stone. On the right side, this area is bounded by a well-defined margin, which runs between the posterior boundary

of the antenna, and the inner of the two endognaths. On the left side, its well-marked curved boundary is distinguishable between the antenna and the broken edge of the stone.

Towards the junction of the middle and anterior thirds of the left lateral edge, a long, flattened, filiform appendage (*c*) comes off from the carapace. On the right side, the remains of two such appendages, with, perhaps, traces of a third, are visible (*x*). They come off close to the two endognaths, and one might be inclined to suppose them all organically connected with the latter, were it not for the independent appendage on the opposite side.

In the other, smaller, half of the specimen the only points to be noted are, the greater distinctness of the right boundary of the "sculptured area" in front of the carapace, and of the right (here left) filiform appendages. I am strongly inclined to think that the "sculptured area" in this fossil is the epistoma. The interpretation of the filiform impressions is more difficult. That on the left side *seems* to be attached directly to the carapace, and in that case might be a second antenna. If this be its nature, the impressions on the other side may be the corresponding appendage and the palps of the endognaths. On the other hand, it must be remembered that there is no independent evidence of the existence of a second antenna in the genus, and that the position of the filiform appendage on the left side may be purely accidental.

4. The two singular fossils figured in Plates XII. [Plate 23] fig. 16, and Plate XIII. [Plate 24] fig. 16, are the only remains, which, from their sculpture, may be, with every probability, referred to *Pterygotus*, but which are not as yet referable to their proper place in the organization.

These parts present, at first sight, a striking resemblance to the terminal palette of an ectognath, with a portion of the penultimate articulation. They are described at length in the systematic portion of this Monograph (p. 255); and I will, therefore, only remark in this place that, as the ectognaths of *P. problematicus* and *arcuatus* (the species to which these remains probably belong) have not yet been observed, it is possible that they may be their distal joints. Pending sufficient proof that such is the case, however, it must be borne in mind that they differ in several important respects from any ultimate and penultimate joints of an ectognath at present known. The only alternative which suggests itself is that these parts may have been thoracic or abdominal appendages.

5. The fossil figured in Plate XIII. [Plate 24] fig. 17, is evidently crustacean, but it exhibits no character by which it can be

identified as a part of a *Pterygotus*. It is a broad quadrate plate, abruptly truncated on two of its opposite sides, one of which is much longer than the other, and having the other two margins equal and rounded. Two folds or ridges run from one truncated edge to the other, and divide the plate into three lobes, a median and two lateral. The median lobe presents a series of curved lines or ridges disposed symmetrically on either side of the median line. Similar folds in the one lateral lobe are more or less symmetrically arranged with regard to those on the other lobe.

The shorter truncated margin of the plate presents two impressions, like the remains of articular surfaces, and there are similar impressions at the outer extremities of this margin. Of these, that on one side gives attachment to a long jointed appendage presenting six distinct articulations. The basal joint is short and much wider than the others. The distal edge of the fourth presents a series of strong spines, the sixth has the form of a curved claw.

I know of only two crustacean structures with which this body can be compared, the one is a carapace, the other the swimming limb of a copepod with its coalesced, lamellar, basal joints greatly developed (compare, Plate XVI. [Plate 27] fig. 7).

Systematic Position of Pterygotus.—In comparing *Pterygotus* with other crustaceans, for the purpose of determining its systematic position and relations, several of the largest and best defined orders of the *Crustacea* may at once be left out of consideration. *Pterygotus* is clearly not one of the *Trilobita*, *Cirripedia*, *Ostracoda*, *Edriophthalmia*, or *Stomapoda* (if we restrict this order to these *Crustacea* which have pedunculate eyes, and distinct and movable ophthalmic and antennulary somites). Nor are there any known *Branchiopoda* to which these great extinct crustaceans have relations of affinity, so that if they are to be referred to any existing order, it must be either that of the *Podophthalmia*, that of the *Copepoda*, or that of the *Pœcilopoda*.

The first step towards determining the systematic place of *Pterygotus*, therefore, is to consider the reasons for and against the assignment of a position in either of these orders to them.

To those who are acquainted only with the ordinary *Podophthalmia*, the discussion of the affinities of *Pterygotus*, with forms in every way so distinct, may seem superfluous; and there is assuredly little enough in common between a crab or a shrimp and their palæozoic congeners; but there are one or two sections of the *Podophthalmia* which, while they still hold fast by the typical characteristics of their order, become so modified in many important

particulars, as to require careful consideration in relation to the forms at present under consideration. These are the *Diastylidæ* or cumoid *Crustacea.*

The typical genera of this group were first described by Mr. H. Goodsir, and they have since been the subject of excellent essays by Kröyer and Spence Bate.

Cuma Rathkii (Plate XVI. [Plate 27] figs. 17, 18) may be selected for description as a good representative of the family. The animal presents anteriorly a short and broad carapace, having its outer and lateral edges rounded and sloping into a bifid, median, anterior, rostrum-like prolongation. The longitudinal fissure of this process divides posteriorly on the carapace, so as to embrace the anterior part of a more convex median lobe, which represents the tergal region of the head. The bifid median prolongation is not, as it appears to be, a frontal rostrum, but it is formed by two lateral processes of the carapace, which come forward and are applied to one another in front of the head.

The carapace is succeeded by five broad thoracic somites, and these by six, narrower and longer, abdominal somites and a telson. The sixth abdominal somite has styliform appendages, but in the female there are no other abdominal limbs, and in the male such as exist are few and rudimentary.

Of the appendages, the eye is median, sessile, and not easily made out in spirit specimens; there are a pair of antennules, a pair of antennæ and of mandibles, two pairs of maxillæ, and eight pairs of thoracic appendages; there is a small labrum and a bifid metastoma; but these parts have too little resemblance to any of the organs of *Pterygotus* to need description in this place.

The most interesting feature about this crustacean in reference to the present inquiry, however, is the ornamentation with which the body and many of the appendages are covered. The surface of the integument appears in many parts irregularly reticulated, but elsewhere the reticulations assume the form of a regular squamous sculpture, singularly like that upon *Pterygotus*, but on a very much smaller scale.

The general form of the body and the paucity of abdominal members, combined with the peculiar sculpture exhibited by the *Diastylidæ*, attracted my attention strongly when, on a former occasion,[1] I endeavoured to trace the affinities of *Pterygotus*. Following the line of inquiry thus suggested, I pointed out that in many

[1] Quarterly Journal of Geological Science, vol. xii. 1855.

Schizopoda and *Stomapoda*, such as *Mysis*, *Phyllosoma*, and *Erichthys*, either the abdominal or some of the posterior thoracic members, or both, became abortive, and that in the larval condition of some *Podophthalmia*, even the sixth pair of abdominal appendages remains undeveloped, and the abdomen is wholly devoid of limbs. In the larval *Brachyura* or *Zoeæ* all the appendages but the gnathites and antennæ are rudimentary, and the long palpiform maxillipedes are (in addition to the abdomen) the only organs of propulsion. The larval lobster (before hatching) is similarly deprived of abdominal appendages, it possesses a disproportionately large labrum, and a metastoma, which is only slightly emarginate anteriorly, and very large in proportion to the other buccal organs, as compared with its adult state.

In the paper referred to, I laid considerable stress upon the analogies, which, from what has been said, may be readily enough apprehended, between *Pterygotus* and the *Diastylidæ* and larval *Podophthalmia*. Renewed examination of the specimens and of the far more extensive materials which have since presented themselves, aided by a careful investigation of the characters of the recent *Copepoda*, has shown me, however, that at least as strong a case might be made out for the relegation of the *Pterygoti* to the latter order. (See p. 202, note.)

The evidence which has led me to this conclusion can only be appreciated when the structure of the *Copepoda* is fully understood. I will, therefore, proceed to give a brief account of that structure, and I am the more willingly led to do this as I have found it difficult, notwithstanding the valuable labours of Milne Edwards, Baird, Dana, and others, to arrive at a clear and connected view of the anatomical characters of this difficult group.

The genus *Calanus*, containing a large number of marine species, is perhaps best fitted to furnish a typical illustration of copepod anatomy. The species represented in Plate XVI. [Plate 27] fig. 1, was taken in the North Atlantic. It is about one-eighth of an inch long, and (after preservation in spirit) has a lightish brown colour. The body presents a large carapace anteriorly, succeeded by a number of thoracic and abdominal segments. The cephalo-thorax has the form of a long oval, truncated and slightly excavated behind, the postero-lateral angles of its last segment being but very slightly produced. The abdomen has not a third the length of the head and thorax, and is terminated by two elongated lobes provided at their extremities with long setæ. The antennules are as long as the body. The cephalo-thorax consists of six segments, the anterior of which is

about equal to the three following ones in length, and forms a carapace. The abdomen presents four obvious segments, but the first appears to consist of two somites united together, and it is probable that the two terminal styliform lobes may represent a somite, in which case there would be six somites in the abdomen. The anus opens between the bases of the terminal processes.

The carapace is not prolonged, either along its posterior margin or laterally, but merely overlaps the tergum of the succeeding somite in the ordinary manner. Anteriorly, it extends beyond the bases of the antennules, and is produced forwards and downwards, between them, into two delicate pointed processes, slightly constricted at their bases, which are about equal in length to the two basal joints of the antennules. The latter are slender, of even thickness, and divided into twenty-four setose joints.

An endophragm, or inflexion of the chitinous integument, distinctly separates the sternum of the antennulary, from that of the antennary, somite. Viewed laterally, the former appears concave, its posterior portion sloping backwards and downwards at an angle with the anterior. The anterior half of the antennary sternum, on the other hand, is very convex, while its posterior half is produced into an abrupt conical protuberance, behind which it passes into a broad plate, with a free, convex, posterior edge. This projecting mass developed from the antennary sternum appears to me to represent both the epistoma and the labrum of decapod Crustacea.

Viewed from below (Plate XVI. [Plate 27] fig. 2) the part described has the aspect of a very broad, almost triangular plate, occupying nearly the whole width of the antennary sternum, and presenting a prominent median portion and two lateral alæ, which slope away backwards and upwards. The posterior portion of the median lobe is rounded and somewhat expanded at its extremity, and the lateral edges of the expanded end are provided with fine setæ, which extend over its superior face for a short distance. This conjoined epistoma and labrum forms the anterior boundary of the oral vestibule; its inner face is beset with short setæ, and a short median tooth, rounded at its extremity, projects backwards in the middle line.

Posteriorly, the oral vestibule is bounded by a quadrate plate, the metastoma, directed forwards and downwards, and having about two-thirds of the width of the labrum. As the sterna of the two somites which immediately succeed the mouth, viz., the mandibular and the first maxillary, are not distinctly separated from one another; it is difficult to say from which this plate arises. I am inclined to

think, however, that it is really a production of the maxillary sternum, as its posterior boundary lies behind the level of the anterior margin of the base of the maxillæ. The free anterior extremity of the plate is deeply divided, by a wide median excavation, into two lobes, which are provided with many short and fine setæ. A little, accessory, setose, lobule is also developed from the inner surface of the plate on each side.

A well-developed endophragm separates the sternum of the first maxillary, or second post-oral, somite from that of the rest. From the mouth to the posterior edge of this, the third post-oral somite, the sternal surface slopes gradually downwards; but beyond this point, or in the fourth post-oral somite, the sternum makes an abrupt projection downwards and then passes backwards, with a general parallelism to the axis of the body, for the rest of the extent of the cephalo-thorax.

The antennæ are about as long as the proximal nine or ten joints of the antennules. They consist of a short basal portion supporting two branches of about the same length. The basal portion is three-jointed, the inner branch two-jointed, the outer multiarticulate.

Neither antennules nor antennæ are chelate or sub-chelate in either sex.

The mandible (fig. 3) consists of a basal joint and a palpiform appendage. The outer half of the former is quadrate, convex inferiorly, and presents, posteriorly and externally, a curved articular process; the middle of the basal joint is a little constricted and flattened, while its internal portion widens again, and ends in a truncated, toothed edge. The teeth are continuous with the blade of the mandible, not articulated with it. The palp springs from an excavated surface on the anterior and superior face of the quadrate outer division. Its proximal joint is short and rounded. The next is the longest, and as broad as or broader than the basal joint, and wider distally than proximally. At the distal end it supports two branches, the outer of which is obscurely five-jointed; the inner two-jointed. The toothed and cutting extremities of the basal joints of the mandibles pass between the labrum and the metastoma, and bite against one another in the middle line. Those of the maxillæ lie behind the metastoma. The first maxilla (fig. 4) is nearly of the same size as the mandible. Its basal joint is produced internally into a large curved process, whose inner edge is beset with strong articulated setæ, which might almost be called elongated teeth, were they not setose along their edges. Succeeding this

articulation is a broad joint produced internally into a narrow, transversely elongated, flattened process, terminated by elongated setigerous setæ externally, into a broad flat plate bearing eight or ten extremely long and strong setigerous setæ ; five other obscurely marked joints follow these two.

The next appendage (fig. 5) is not quite so long as that just described ; it is obscurely divided into seven joints and tapers to its extremity, which, like its inner edge, is provided with very long and strong setæ. The inner setæ are by far the stronger, and are directed forwards so as nearly to reach the mouth.

The fourth post-oral appendage (fig. 6) is more than twice as long as the third. It consists of a short and strong, subcylindrical, basal joint, beset along its inner margin with a row of very long setigerous setæ, and having a rounded projecting inner distal angle. One long and five short gradually diminishing articulations follow this.

To this appendage succeed the five pairs of swimming feet (fig. 7), of which the first and the last are smaller than the intermediate ones. Each natatory limb consists of a stem (protopodite) and two branches (endopodite and exopodite). In the former a long proximal and a short distal joint are distinguishable. The proximal joint is united, for a considerable part of its length, to its fellow on the opposite side by a flattened plate, continuous above with the sternum, and thickened by a spatulate ridge in the middle line.

The distal joint has the inner half of its terminal margin more produced than the outer. The former bears a shorter (endopodite), and the latter a longer, three-jointed branch (exopodite). The terminal articulation is the largest, and is provided with long and strong setæ.

The inner edges of the basal joint of the protopodite of the fifth pairs of these feet are beset from their distal extremities to the uniting plate with a series of short, but strong and pointed teeth.

On considering the structure of *Calanus* with reference to the general plan of the *Crustacea*, I may observe, in the first place, that of the twenty typical somites, only eighteen, at most, appear to be represented. We may reckon one, for the eyes ; two, for the antennules and antennæ ; four, for the four pairs of post-oral appendages ; and five, for the swimming feet, making, in all, eleven, provided with moveable appendages. Then, if the first segment of the abdomen be really formed, as there is much reason to believe it is, by the coalescence of two somites, and if the two caudal styles really represent another, we shall have six somites in the abdomen, making up the sum total to eighteen.

This number cannot by any means be made out in all *Copepoda*, but I know of no members of the order which exceed it. Different opinions have been entertained with respect to the grouping of these somites into cephalic, thoracic, and abdominal. The eyes, antennulæ, antennæ, and the two anterior pairs of post-oral limbs, and with them their somites, are indeed universally admitted to belong to the head; but the two following appendages are considered by some to be maxillæ, by others to be maxillæ and maxillipedes; by yet others to be maxillipedes and anterior thoracic limbs.

The simplest and most natural view appears to me to be, to regard the third pair of post-oral appendages as the homologues of the second maxillæ or last cephalic appendages, while the fourth post-oral appendages are thoracic members. In this case there will be six pairs of thoracic appendages, as in the *Cirripedia*. If we inquire what has become of the two thoracic somites which are unrepresented by appendages, three probabilities present themselves:—1. They have remained undeveloped at the anterior end of the thorax; or, 2, they have remained undeveloped at the posterior end of the thorax; or, 3, the two somites which are so closely united together as to appear as one segment, commonly regarded as the first of the abdomen, belong in reality to the thorax. This view might be supported by the position of the reproductive apertures which open behind the second of these somites, that is, on this hypothesis, in that position immediately behind or at the posterior part of the thorax, which is so common to them in *Edriophthalmia*, *Pœcilopoda*, and male *Podophthalmia*. If this view be correct, (but I would expressly state that it is put forth only tentatively,) it is the abdomen alone which is shorn of its due proportions in *Copepoda*.

Such is the structure of a typical copepod. The modifications observable in the order, of importance for my present purpose, affect,—1stly, the form of the body; 2ndly, the character of the eyes; 3rdly, the form of the antennules and antennæ; 4thly, that of the labrum and metastoma; 5thly, the number of the thoracic appendages.

1. The body usually has a general resemblance in outline to that of *Calanus*, the abdominal somites commonly presenting a marked and immediate diminution in transverse diameter when compared with those of the cephalo-thorax. In the beautiful *Sapphirinæ* (Plate XVI. [Plate 27] fig. 19, however, the passage from the cephalothoracic to the abdominal somites is quite slow and gradual.

2. In most *Copepoda* the eyes are so closely united as to appear single, and the region of the carapace which overlies them is not so modified as to deserve the name of a distinct cornea. But in the genus *Sapphirinæ* (Plate XVI. [Plate 27] fig. 19), there are two small single corneæ approximated together in the middle of the dorsal surface of the carapace ; and a still more interesting modification of the visual organs is presented by *Corycæus* (Plate XVI. [Plate 27] figs. 8, 9). Here two great, oval, spectacle-like, corneæ are situated, one on each half of the anterior rounded margin of the carapace.

3. The antennules and antennæ vary very much in form. In many *Copepoda* they are so constructed as to subserve prehension, either for sexual or other objects. The antennules are thus specially modified in the males of *Pontella* and *Cyclops*, while in *Corycæus* these organs remain simple; but the antennæ (III.'), are, in both sexes, converted into formidable weapons. It will be observed, however, that prehension is effected by the folding of the ultimate upon the penultimate joint, not by the biting of the apex of the ultimate joint against the prolonged distal angle of the penultimate. It is a subchela such as is found in *Amphipoda* and *Stomapoda*, not a chela like that of *Podophthalmia* and *Pœcilopoda*.

4. The plate, which corresponds with the conjoined epistoma and labrum of decapod *Crustacea*, is very large in all the *Copepoda* I have examined. Its form and proportions in *Calanus*, *Corycæus*, and *Pontella* are shown in (Plate XVI. [Plate 27] figs. 2, 9, 11). In the last-named genus it exhibits, as Milne Edwards has pointed out in his great work on the *Crustacea*, the remarkable peculiarity of being divided into three lobes, of which the middle is the smallest, and constitutes a kind of tongue-like projection (fig. 11).

5. The metastoma of *Calanus*, as has been stated above, is excavated anteriorly by so deep and wide an emargination, that it almost appears to consist of distinct lobes. In *Pontella*, on the other hand, the metastoma is a large flattened plate, whose terminal emargination, though wide, is not deep (fig. 11).

6. In *Calanus*, nine pairs of post-oral appendages have been found, the greatest number possessed by any masticating copepod. In *Corycæus* and *Cyclops* this number is reduced to eight, and of these the last is occasionally so much atrophied as to be hardly distinguishable. We have thus evidence of a certain tendency towards a diminution of the number of thoracic appendages in this order.

The study of the development of the *Copepoda* shows that this

is no more than might be expected, when we take into consideration how common a thing it is, for some form of a group to retain more or fewer of the characters usually found only in the young of that group; and perhaps the only subject for astonishment is that adult *Copepoda*, with still fewer limbs, have not yet been discovered. A Copepod just hatched is, in fact, a very different creature from the adult, as has been known since the observations of Jurine upon *Cyclops*.

Rathke, who has devoted particular attention to the development of the embryo in this genus, maintains that of the three pairs of locomotive appendages, with which alone the young is endowed when it leaves the egg, the two anterior eventually become the antennules and antennæ, while the posterior are neither the mandibles nor the first pair of maxillæ, but the rudiment of the "mains" of Jurine. The young *Cyclops* is in addition provided with a large epistomo-labral plate. Its further changes consist chiefly in the elongation of the body, and the gradual and successive acquisition of the thoracic members.

The resemblances of *Pterygotus* to the *Diastylidæ* do not extend to the most important and characteristic features of its organisation, and even were we to combine together into one form all the analogous peculiarities which have been noted in these, in *Stomapoda*, in *Schizopoda*, and in larval *Podophthalmia*, we should not get a sufficiently near approximation to *Pterygotus* to justify the arrangement of the extinct genus in either of the orders of the higher *Crustacea*. As I hinted above, however, a stronger case might be made out for the *Copepoda*. Combine the body of *Sapphirina* with the eyes and antennæ of *Corycæus*, the mandibles and maxillæ of *Calanus*, the epistoma and metastoma of *Pontella*, and the total number of appendages of a copepod larva, and something marvellously like a *Pterygotus* would be produced. But such an animal would not be a *Pterygotus*, and even if it were, it would differ so widely from any of the known *Copepoda*, that its association with the members of that order would be a step of very questionable propriety. Confining the argument to known and existing *Copepoda*, the differences between them and *Pterygotus* are sufficiently striking.

No Copepod has truly chelate antennæ or antennules, and none present any approximation to the remarkable teeth with which the chelæ of *Pterygotus* are beset. All known Copepods have large thoracic appendages; no trace of such organs has yet been discovered in *Pterygotus*.

No Copepod, so far as I know, presents so great a number as twelve free segments behind the carapace.

No Copepod has its appendages reduced to so few as three or four pairs, nor, in any, is one pair of the post-oral cephalic appendages converted into the chief organ of locomotion.

The *Pœcilopoda* (Plate XVI. [Plate 27] fig. 13) are I believe the only *Crustacea* which possess antennary organs like those of *Pterygotus*, and, like them, have the gnathites converted into locomotive organs, want the appendages to the sixth abdominal somite, and present on some parts of the body a remotely similar sculpture. In this order, however, we find but a small labrum,—a rudimentary metastoma,—a very differently constructed body, and a large number of appendages, both thoracic and abdominal, characters which effectually preclude the association of the extinct *Crustacea* under discussion with this type.[1]

The palp of the mandible of *Nebalia* (Plate XVI. [Plate 27] fig. 10) is, in its proportional size and form, not unlike that of *Pterygotus anglicus*, but this is the sole resemblance of importance which I can detect between the *Branchiopoda* and the *Pterygoti*.

While the relations of the *Pterygoti* with the great majority of other *Crustacea* are such as, in my mind, fully to justify their ordinal separation, there is one small and extinct group, having a similar geological range, with which they are undoubtedly closely connected. This is the genus *Eurypterus* of Harlan, of which many species have now been brought to light. Putting together the descriptions of Harlan, Eichwald, Roemer,[2] and others, with the results of a personal inspection of some species recently described by Mr. Salter, I can only arrive at the conclusion that, in its general form and structure, *Eurypterus* very closely resembled *Pterygotus*, differing from it however as *Sapphirina* differs from *Corycæus*, viz., in having the eyes submedian instead of marginal. The ectognaths of *Eurypterus* appear to have been constructed upon precisely the same plan as those of *Pterygotus*, and its thoracic and abdominal members would seem to have been equally undeveloped.[3] Eichwald describes

[1] If the abdominal somites or the Carboniferous *Bellinurus*, &c. were really free, they would present a certain approximation to the *Pterygoti*. Indeed, the evidence that these Csrboniferous *Crustacea* were true *Pæcilopoda* is, to my mind, anything but conclusive.

[2] *Ferd. Roemer.* Ueber ein bisher nicht beschriebenes Exemplar von Eurypterus aus Devonischen schichten des Staates New York in Nord-Amerika.—Dunker und von Meyer's Paleontographica, b. 1, 1851, p. 190.

[3] Eichwald's representation of the under surface of the head is terribly diagrammatic. If it be a correct representation of an actual object, it affords evidence of only three pairs of appendages. His "two large, almost semilunar, lateral parts" appear to me to be the basal

twelve segments behind the carapace (though only eleven are represented in his figure). Two pairs of slender jointed appendages are figured both by him[1] and by Harlan in front of the ectognaths; but no chelate antennæ are represented, and the connexions of the jointed appendages are not made out. The characteristic sculpture is well exhibited by *Eurypterus*. Even if the chelate antennæ are really absent in *Eurypterus*, it must be remembered that these are organs particularly liable to variation among even closely allied genera of *Copepoda*.

Leaving the determination of the precise differences between the *Pterygotus* and *Eurypterus* to future investigators, their resemblances to one another, and their common differences from all other *Crustacea*, are sufficiently important to justify their association into a distinct order—the "*Eurypterida*," which may be thus defined: *Crustacea* with numerous free thoracico-abdominal segments, the penultimate, and probably all the rest of which, are devoid of appendages; with the anterior somites united into a carapace, bearing a pair of large marginal or subcentral eyes; with a very large epistoma and metastoma; with three, or four pair of moveable cephalic appendages, the posterior of which form great swimming feet, and with the integument characteristically sculptured.

Of the mode of life of these extinct *Crustacea* we know nothing, but we may conjecture that it was their habit sometimes to creep along the bottom of the waters which they inhabited, like the *Limulus* of the present day, sometimes to propel themselves by the rapid flexion of their great swimming feet, aided perhaps by the sudden extension of their free segments.

No existing or extinct crustacean has so massive a body as *Pterygotus*, some species of which there is every reason to believe attained a length of at least five feet; but mass, in an active animal, involves large muscles, and these require solid *points d'appui*. Hence we may conclude that the integument of the *Pterygotus*, thin and fragile as are its remains, possessed a great amount of firmness in the recent state.

That the singular thinness of the fossil test, constituting a mere

joints of the ectognaths, while the middle ovate "under lip" has just the position and general form of the metastoma. Add to these the triangular "upper lip," and the resemblance to *Pterygotus* becomes not a little striking.

[1] Roemer states that his *Eurypterus* also had twelve free segments behind the carapace. The eyes borne by the latter were uniform and not faceted; only two appendages, both on the left side, remained. The posterior had the general structure of the ectognathary limb of *Pterygotus*. The anterior is slender, four-jointed, and perhaps terminated in a chela.

papyraceous film, is not inconsistent with great solidity in the recent condition, is shown by the existing *Limulus*, whose leathery integument is thick and hard enough to give firm attachment to very large and powerful muscles, and yet contains so little calcareous matter, that when dried and subjected to such pressure and decomposing influences as have operated upon the *Pterygoti*, it would probably be hardly more bulky.

It is not without interest to find that the skeleton was as perishable in the *Crustacea* as in the *Vertebrata* of the period in which the *Pterygoti* flourished.

Note, p. 193.—So long ago as 1840, Milne Edwards indicated the relations of *Eurypterus* with the *Copepoda* in the following words:—"The fossil *Crustacea* of which M. Dekay has formed the genus *Eurypterus* appear to have much analogy with *Pontia* (*Pontella*) and *Cyclops*, and also seem in some respects to form a link between these animals and the *Isopoda*."—Hist. Nat. des Crustacés, t. iii. p. 422.

XII

BRITISH FOSSILS

Part II.—DESCRIPTION OF THE SPECIES OF PTERYGOTUS

By J. W. SALTER, F.G.S., A.L.S.

Memoirs of the Geological Survey of the United Kingdom, Monograph I., 1859, *pp.* 37—105.

Pterygotus. Gen. Ag.

The generic characters have already been detailed in the introductory portion of this memoir. It is only necessary here to give them in brief, and point out the two very distinct sections or sub-genera into which the group may be divided. These sections are indicated by the form of the head, the position and outline of the eyes, the shape of the labrum and palpi, and probably, too, by that of the terminal abdominal segments.

Genus PTERYGOTUS, Agassiz, 1844. (Class Crustacea, Order Eurypterida). Carapace small, semi-oval or subquadrate, with lateral eyes, followed by 12 body segments unfurnished with appendages, the twelfth being a large telson, pointed or acuminate, or blunt and bilobed; epistoma large, deeply trilobed; antennæ of few (4) joints, strongly chelate; mandibles (and maxillæ?) with palpi of 6 or more joints; metastoma ovate, large, notched anteriorly; a large pair of ectognaths, their terminal joints expanded for swimming, and the great foliaceous basal joint furnished with an inner serrate lobe or process.

Section 1. Carapace semi-oval, produced in front beyond the elongated lateral eyes; labrum with its middle lobe ovate; palpi linear, simple; bases of swimming feet foliaceous and overlapping each other; the succeeding joints attached posteriorly. [Terminal joint or telson truncate or bilobed; the penultimate not expanded.] 3 species. *P. bilobus*, &c.

Section 2. *Pterygotus* proper. Carapace quadrate or subquadrate, seldom semi-oval or produced in front; eyes large, round, placed far forwards; labrum transverse, its middle lobe sagittate at base; palpi with tumid joints, fringed, or branched; bases of swimming feet not overlapping each other; the succeeding joints attached more forward than in the last section. [Telson ovate, apiculate, or greatly produced, the penultimate joint expanded.] 12 species. *P. anglicus*, *P. gigas*, &c.

It will be seen that these sub-genera contrast in nearly all points. The production, however, of the front margin into a semicircular form in one of the true *Pterygoti*, *P. gigas*, and the possibly emarginate apex to the long ovate telson of that species, show that these characters are not without variation. Yet even in this case the

large rounded eyes and wide expanded penultimate body joint indicate that the species belongs to Section 2. The forward position of the eyes is extravagantly shown in such species as *P. acuminatus*, in which, too, the telson attains its greatest degree of elongation. *P. stylops* has a similar but even more prominent eye.

The overlapping of the basal joints of the swimming feet in Section 1, and the attachment of the other joints lower down, may be characters of less importance, but they are associated in *P. bilobus* and *P. inornatus* with the characteristic elongated eyes, and the central lobe of the labrum is ovate, instead of sagittate in these species. The terminal joint or telson is also of like shape in *P. bilobus* and *P. Banksii*, the only two species of the sub-genus in which it is known.

Although, therefore, *Himantopterus* has been restored to *Pterygotus*, the character in which it was formerly supposed to differ, viz., the lateral eyes, being common to both, it is advisable to keep the above two sections or subgenera distinct; and it may hereafter be necessary, when we have a more complete knowledge of the several species, to reinstate the section as a genus, in which case the name *Erettopterus*[1] will be appropriate. It is certainly more remote from *Eurypterus* than is *Pterygotus* proper, and some unpublished species of the former have the eyes so far outwards as to make a near approach to the section or subgenus here described. The shape of the antennæ, however, is quite enough to separate them; and the telson of *Eurypterus*, so far as it is known, is linear,[2] or linear lanceolate.

Pterygotus is known now to range from the Upper Llandovery Rock (or May Hill Sandstone) through all the overlying Upper Silurian Rocks into the Cornstones of the Old Red Sandstone, though it is but rare above the base of the last-named formation; its metropolis seems to be at the point of transition between the Silurian and Devonian formations. Fifteen species are known.

Eurypterus began not quite so early, being first met with in the Upper Ludlow Rock, and thence, becoming abundant in species (though of small dimensions) in the passage beds at the base of the Old Red Sandstone, attained its maximum of size in the upper portions of that formation and the base of the carboniferous rocks, after *Pterygotus* had apparently ceased to exist. (See Quart. Journ. Geol. Soc. for 1859, vol. xv. ined.) About sixteen species are known.

[1] ἐρέττω, for ἐρέσσω, to row; instead of *Himantopterus*; see note p. 175.

[2] *Stylonurus*, Page, has a similar form, but possesses thirteen body segments and long linear swimming feet.

PLATE I. [PLATE 12] FIGS. 1–12.

SECTION 1.

PTERYGOTUS BILOBUS.

P. 8-uncialis, sublævis, capite semielliptico, corpore abbreviato antice latiori, caudâ oblongâ carinatâ emarginatâ.

SYNONYM. *Himantopterus bilobus*, SALTER, in Quart. Journ. Geol. Soc. vol. xii., p. 29, fig. 1; also "Siluria," 2nd edition, p. 155, foss. 21. PAGE, in Advanced Textbook, p. 135, fig. 1.

We have more perfect materials for this species than for any of the rest,—above twenty specimens, many of them full grown, and showing all the segments; in some the head with its elongate eyes and few-jointed antennæ; the long palpi in others; two show the serrated jaw feet beneath the carapace with the swimming joints attached; the post-oral plate is *in situ* in another; and there are numerous detached specimens of all the appendages except the palpi, of which last we should know but little but for the explanation afforded by the next described species.

The geological position of this and the other *Pterygoti* from Lesmahago has been fully given by Sir R. I. Murchison, our Director-General, in the 12th volume of the Quarterly Journal of the Geological Society, p. 23. The occurrence with them of a small spiral shell and a *Lingula*, identical with those of the Downton Sandstones of Shropshire, justifies the reference of the strata to the age of the Uppermost Ludlow Rocks, while not one of the species is identical with those of the border counties of Wales, either in the Ludlow Rocks or in the Passage Beds which immediately overlie them. This fact is remarkable, and may serve to indicate the probability of a vast number of species yet to be discovered.

Description.—The general form of *H. bilobus* is elongate-oval in front and attenuated behind (resembling a good deal the outline of a *Palæoniscus* or other fish). The thorax is not easily distinguished from the abdomen, into which it is attenuated, the greatest width being about the third or fourth segment; its segments are widely transverse, those of the abdomen become less and less so, till the last but one is nearly square; the tail joint is oblong and emarginate, and narrowest of all; the antennæ are slender and long, the swimming feet narrow, the palpi filiform; and these general characters, taken together with the small size (seldom nine inches long), will easily

distinguish the present species from the following. The different portions may now be more minutely noticed.

The carapace, one inch and a quarter in length, is half-oval, only one-fifth wider than long. The position of the long eyes is very forward on the sides, and they somewhat interrupt the general oval contour. They are broadly crescentic and convex, placed half below (fig. 4 *c*) and half above the margin of the head, and their extreme length is rather more than half that of the head. No lenses can be seen with the naked eye, but when magnified the appearance is that given in fig. 4 *d*.

Body Segments.—The body in well-preserved individuals is barrel-shaped in front, the anterior or thoracic segments, taken together, measuring about one inch and three-quarters in length by one inch and a quarter broad. They are widely transverse, the anterior one being fully four times as broad as long, or even more.

The second ring, as seen in a specimen not here figured, is five times as wide as it is long, the central part gently arched forwards in the middle, and at the sides the upper angles are produced forward into blunt lobes,[1] the outer margins being oblique, and their posterior angles are a little produced backward, particularly in the sixth or hindermost thoracic ring.

The remainder, which are here reckoned as abdominal, are gradually narrower, the seventh being only three times as wide as long, the tenth only once and a half, and somewhat narrower at the origin than the posterior edge ; the penultimate (eleventh) is squareish, only a little wider than long, also contracted at the origin and with the outer angles produced to lap over the rounded anterior edges of the caudal joint. A strong carina runs down this segment upon the upper side, but for the lower half only.

The caudal joint (telson) is only two-thirds as wide as long, and nearly double the length of the penultimate one. It is rather wider behind, and strongly emarginate ; a deep furrow takes its origin from the notch, and continues more than half-way up. There is a low keel at the upper end joining that of the preceding segment, but only for a very short distance.

The outer margins of the body and tail segments appear to be quite smooth, not serrate or crenate as in several other species.

The thickness or rotundity of the joints we have no means of ascertaining.

The sculpture is minute and characteristic, but is only visible at

[1] This form of the second segment is common to all the species, see fig. 13 of this Plate, and Plates IV., X., XIII. [Plates 15, 21, 24], &c.

a few points. None has been observed on the head. On the body joints numerous small semicircular plicæ (fig. 2 *a*)—the curve open forwards—cover the surface, but are less conspicuous on the hinder portions of each segment. On the anterior narrow segment they are perhaps most prominent, and on this and some other of the front rings a raised transverse thread-like ridge runs across at about the middle, or a little in advance of it, but does not limit the conspicuous portion of the sculpture.

Under Side of Head, and Appendages.

In three or four specimens, figs. 1, 3, 4, 9, &c., the organs of the mouth, with the antennæ, are *in situ*, and in others the appendages of the head occur so grouped together as to show that they were associated. Fig. 3 appears to have the parts most complete.

Antennæ (fig. 6, &c.)—None have been found more than two inches long by a quarter of an inch broad at the base of the chelæ, the free joint of which is, in antennæ of this size, about six-tenths of an inch long. The base of the fixed finger is but slender, scarcely thicker than the preceding joint, and is shorter than the chelæ, the shafts of which are linear and straight. (Fig. 7 is broader than usual, and may indicate a difference of sex). The points of the chelæ are sharply incurved; their armature is minute, of small and larger teeth.

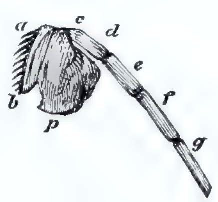


FIG. 1.
Endognath (Mandible), natural size? of *Pterygotus bilobus*, *p*, the basal or attached portion; *c–g*, palpus.

There are apparently but four joints in the antennæ, the basal one small, the second, fig. 7 *b* (both figs. 6 and 7 are wrongly drawn as to the length of the lower joints, from being so much broken), at least five times as long as broad, the fourth (*c*) is the fixed claw and its base, and the fifth the free claw. The articulations of the joints are all oblique.

Endognaths (*Mandibles, &c.*)—The under side of the carapace, of which fig. 4 is the cast, shows the great foliaceous bases (with serrate inner lobes) of the swimming feet (*c*). No mandibles or maxillæ[1] have been discovered beneath these; but in fig. 1, at *c*, the long filiform palpi of one pair of these organs extend right and left of the carapace. They are more elongate than in other species.

A small mandible, found since the plate was engraved, is here

[1] The dilated bases of the swimming feet (ectognaths) were formerly supposed to be the mandibles, and the produced neck-like portion to be jointed; Quart. Journ. Geol. Soc. l. c. This has been set right by Professor Huxley (see Part I.).

given as a woodcut. It is contracted in width as compared with the shape in some other species. The anterior serrate lobe *a* is narrow, and with sharp curved articulated teeth. The lamina *p* is oblique and sub-triangular ; and the palpus, set on rather far back from the serrate border, has a small quadrate basal lobe *c* followed by a longer one *d* ; the third and fourth (*e f*) are linear, and several times as long as broad. The terminal joints are still longer, as seen in Plate I. [Plate 12] fig. 1 *c* (compare this with Plate VII. [Plate 18] figs. 4, 5).

Epistoma and Labrum.—Of the large semicircular piece which lies in front of fig. 1, and which has evidently been shifted from the under side of the head, we can only judge the true position by comparing it with other species (*H. perornatus*, for instance, fig. 16, in which the mid-lobe *a* of the organ is seen to be of an ovate shape) ; also in Plate XV. [Plate 26] fig. 2 *f*, where a similar piece lies in front of the head.

In fig. 1 the semicircular outline probably corresponds to the hinder free margin (of much more angular shape) in the epistoma of *P. anglicus*, Plate III. [Plate 14]. The mid lobe *a* is obscurely marked out, but is of an ovate shape ; its insertion not very clearly seen.

Ectognaths.—Fig. 3 shows these organs in their place at the lower angle of the carapace, drawn forward as for a stroke ; the forward bend of the limb at the fifth joint *ca*, and the great serrate bases *b* indistinctly visible through the crust. Fig. 9, with part of the carapace broken away, has both limbs in place, and figs. 1 and 2 show these natatorial feet laid backward close along the body. Fig. 8, magnified at 8 *a*, is an entire separate ectognath. The several joints of this appendage are :—

Basal Joint (*coxognathite*), figs. 4 *c*, 8 *co.*—The great lower lobe is wide, and of a spherico-triangular shape, the inner margins as well as the outer and base being all convex. The neck is suddenly contracted and short, and the serrate terminal lobe transverse or oblong, greatly oblique and overlapping the opposite edge (not vertical as in *P. acuminatus*, Plate II. [Plate 13]). Its toothed margin is curved and set with thirteen small teeth.

The other joints are attached low down, *i.e.*, below the outer margin of the basal joint, and consist of—

b. (*Basignathite*) short and broad-linear.

i. (*Ischygnathite*) narrow triangular, produced a little at the hinder angle (but not forming a lobe as in Plate VI. [Plate 17] fig. 1).

PLATE I. [Plate 12.]

Section I.—*ERETTOPTERUS.*

Fig. 1. *Pterygotus bilobus* more than half grown; showing the epistoma *a*, antennæ *b*, endognathary palpi *c*, contour of the metastoma *d*, and the ectognath or swimming foot.

Fig. 1a. Outline of the metastoma and the adjacent parts of the same specimen.

Fig. 2. A rather larger specimen; the parts of the head crushed and confused.

Fig. 2a. The sculpture of body rings enlarged.

Fig. 3. Anterior portion of one of the largest individuals; the antennæ are directed forwards; the swimming feet (ectognaths) *in situ*, with their large basal lobes *b*.

Fig. 4. A cast of the sternal side of the carapace, with the basal joints of the ectognaths in place; the large eyes are impressed on the lower surface at *c*.

Fig. 4d. The surface of the eyes magnified.

Fig. 5. A lateral view of the same carapace.

Fig. 6. An antenna; the stem which supports the chela is broken, and its joints are not clearly distinguishable.

Fig. 7. A large antenna (belonging to an individual of different sex?); *b*, the long second joint; *c*, the fixed ramus of the chela; *d*, the terminal or free claw.

Fig. 8. An ectognath or swimming foot, forming one of the same group of appendages from which Fig. 6 is taken; *co*, the large basal joint (coxognathite). See p. 208.

Fig. 8a. The palp of the same limb magnified; *b*, the second joint; *i*, third; *m*, fourth; *ca*, fifth joint (carpognathite), forming in this species the angle of the limb; this or the preceding joint gives origin to the long stylet *t*; *p*, the sixth or penultimate joint (prognathite); *d*, the terminal joint (dactylognathite).

Fig. 9. A carapace, with the swimming feet in place; part of the upper surface is removed.

Fig. 10. A metastoma or post-oral plate. 10*a*. A magnified view of part of its surface.

Fig. 11. The telson or terminal segment of the body, compressed laterally.

Fig. 12. A telson, shortened by pressure in an opposite direction.

Fig. 13. *Pterygotus perornatus*; carapace and six anterior segments of the body; at *b*, the fulcral points are seen; *c*, the rounded posterior edges of the first segment; *d*, its anterior processes.

Fig. 13*. An ectognath or swimming foot; the several joints marked as in Fig. 8*a*; for the figure of a better specimen, see Woodcut 3, p. 214.

Fig. 14. A basal joint of an ectognath, from the same specimen as Fig. 13*; *c*, point of attachment of the remaining joints.

Fig. 15. A metastoma.

Fig. 15a. Its sculpture enlarged.

Fig. 16. *Pterygotus perornatus*, var. *plicatissimus*; carapace, much compressed, and partly broken away, showing what are perhaps the traces of the impressions of muscles (for the ectognaths?) at *b*; *a* is the central lobe of the epistoma; *c*, first body segment.

Fig. 16a. The ornamentation of the carapace, magnified.

Fig. 17. *Eurypterus lanceolatus*, without the carapace, but with the ectognaths or swimming feet in place.

Fig. 17*. Sculpture, magnified.

The above are from the Uppermost Ludlow Rocks, Lesmahago, Lanarkshire, and are in the collection of the Museum of Practical Geology.

The Figures in these Plates are of the Natural Size, unless it be otherwise stated.

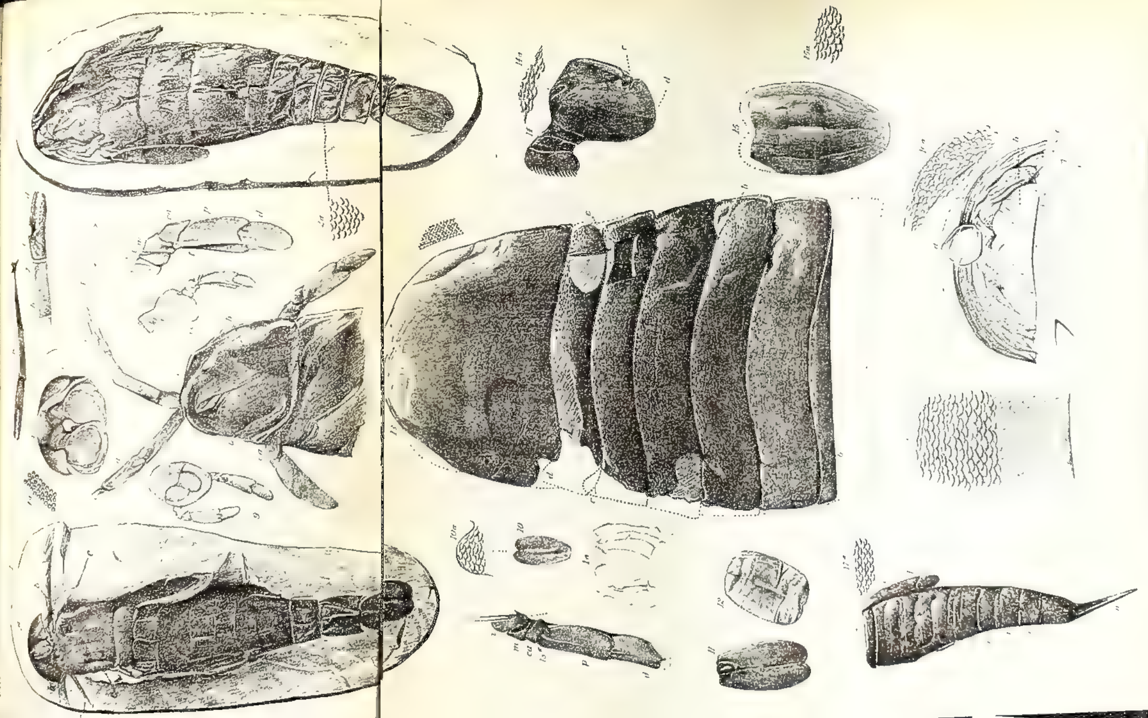


PLATE II. [PLATE 13.]

SECTION 2.—*PTERYGOTUS.*

Fig. 1. *Pterygotus acuminatus.* Outline of the carapace; natural size.

Fig. 1a. The same, reduced nearly one half.

Fig. 2. The ultimate joint or free ramus of the chela of the antenna of an adult (?) specimen. 2*. A few of the teeth magnified.

Fig. 3. Penultimate joint or fixed ramus of the chela of an antenna, probably of this species.

Fig. 4. A metastoma; *a*, the median ridge upon its surface.

Fig. 5. The serrated inner lobe or process of the ectognath.

Fig. 6. Nearly entire basal joint of the ectognath; at *a*, a portion of the sculptured ornamentation, magnified; *co*, the point of attachment for the next joint, *b*, Fig. 7.

Fig. 7. Tergal surface (or that part applied against the body) of the ectognath.

Figs. 8, 9. Sternal or ventral surface of the several joints of its palp.

co, basal joint (coxognathite).
b, second joint (basignathite).
i, third joint (ischyognathite).
m, fourth joint (merognathite).
ca, fifth joint (carpognathite).
p, sixth joint (prognathite).
d, seventh joint (dactylognathite).

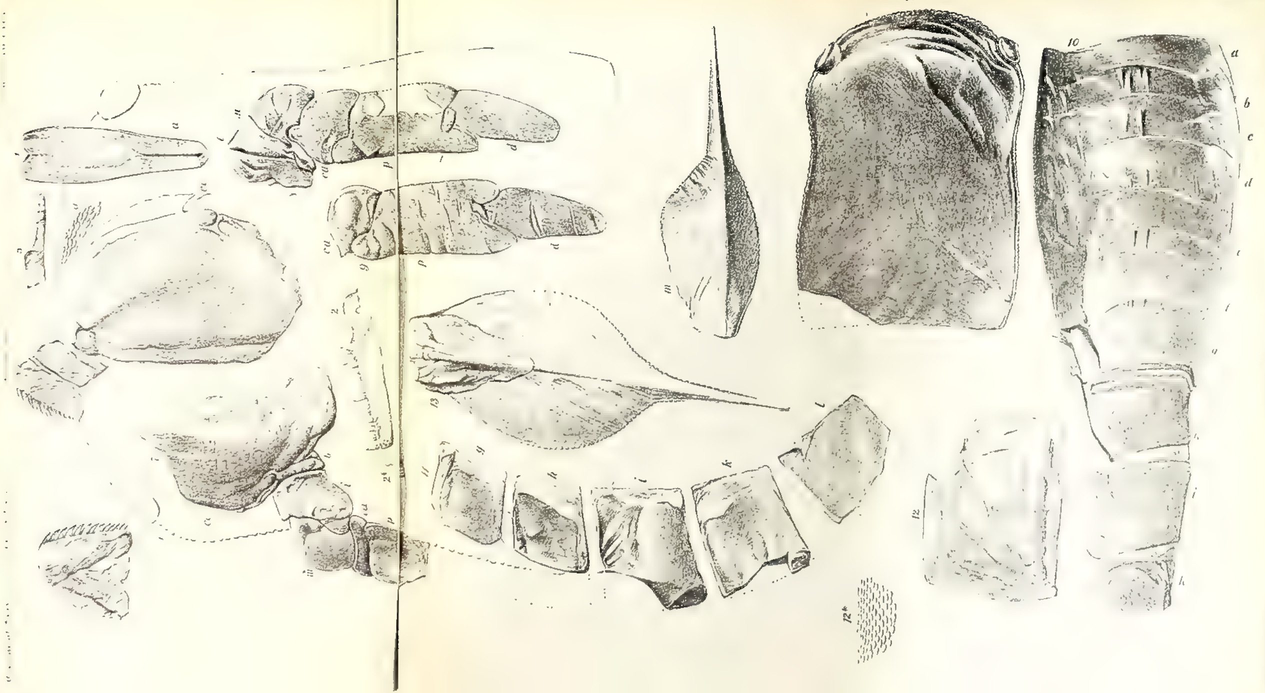
Fig. 10. The segments of the body of a smaller specimen; the segments *a* to *f* have a small double keel, and are probably thoracic; *g*, *h*, *i*, *k*, are probably abdominal rings, and are destitute of these ornaments; the form of the terminal joints *e*, *m*, is shown in Fig. 11.

Fig. 11. Five abdominal rings and the ovate apiculate telson.

Fig. 12. An abdominal ring of a larger specimen. 12*. Its sculpture magnified.

Fig. 13. The telson or terminal joint.

All the above are from Lesmahago, Lanarkshire, and are in the Museum of Practical Geology.



Day & Son Lith^rs to The Queen

PLATE III. [PLATE 14.]

SECTION 2.—*PTERYGOTUS.*

Figs. 1, 1a. *Pterygotus anglicus.* Carapace, three-fourths of the natural size; at *a*, the large eyes, which are represented of their full size and magnified in Figs. 1 *a*, 1 *b*. This specimen is in the cabinet of Lord Kinnaird of Rossie Priory. From Balruddery Den, Perthshire.

Fig. 2. The epistoma (or conjoined epistoma and labrum). The specimen figured by Prof. Agassiz. (Lord Kinnaird's cabinet.)

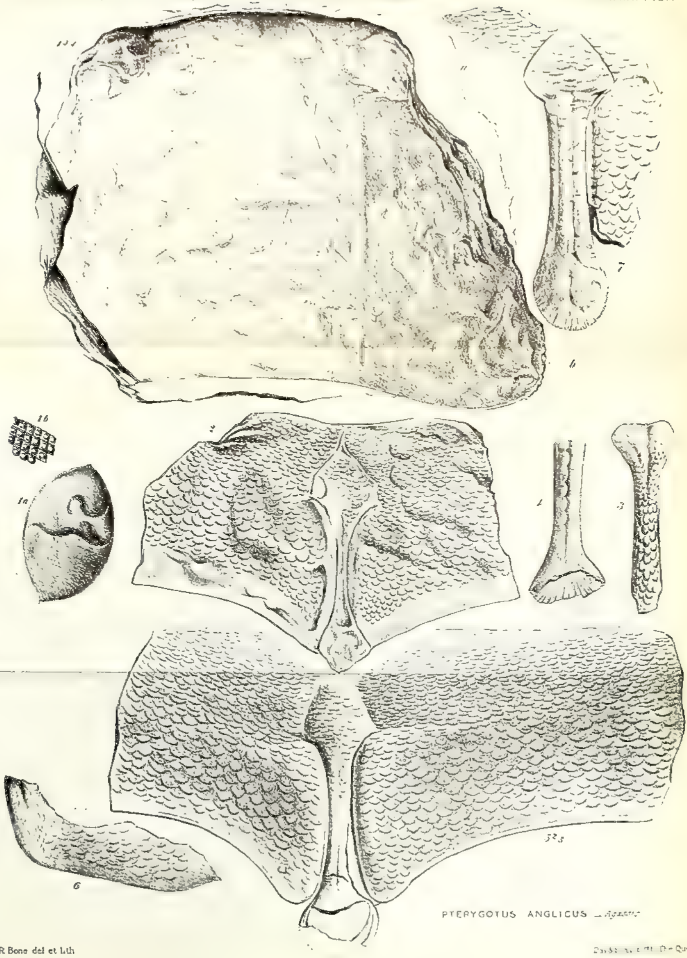
Fig. 3. The central lobe of the epistoma, free from the lateral wings. (Same cabinet.)

Fig. 4. The posterior termination of the central lobe, from a large epistoma. (Same cabinet.)

Fig. 5. A very perfect epistoma, in light grey micaceous sandstone. Leysmill, Forfarshire. (British Museum collection.) Reduced to two-thirds of the natural size.

Fig. 6. The lateral border of the epistoma? Balruddery Den. (Museum of Practical Geology. Presented by Sir P. Egerton, Bart.)

All the above are from the Perth and Forfarshire Paving Stones (Basement or 'Passage Beds' of the Old Red Sandstone).



PTERYGOTUS ANGLICUS _ Agassiz

C R Bone del et lith

PLATE IV. [Plate 15.]

Section 2.—*PTERYGOTUS.*

Pterygotus anglicus. Thoracic and Abdominal Segments.

Fig. 1. The third segment of the body, with projecting antero-lateral processes. A specimen already figured by Professor Agassiz (l.c.) (Lord Kinnaird's cabinet.)

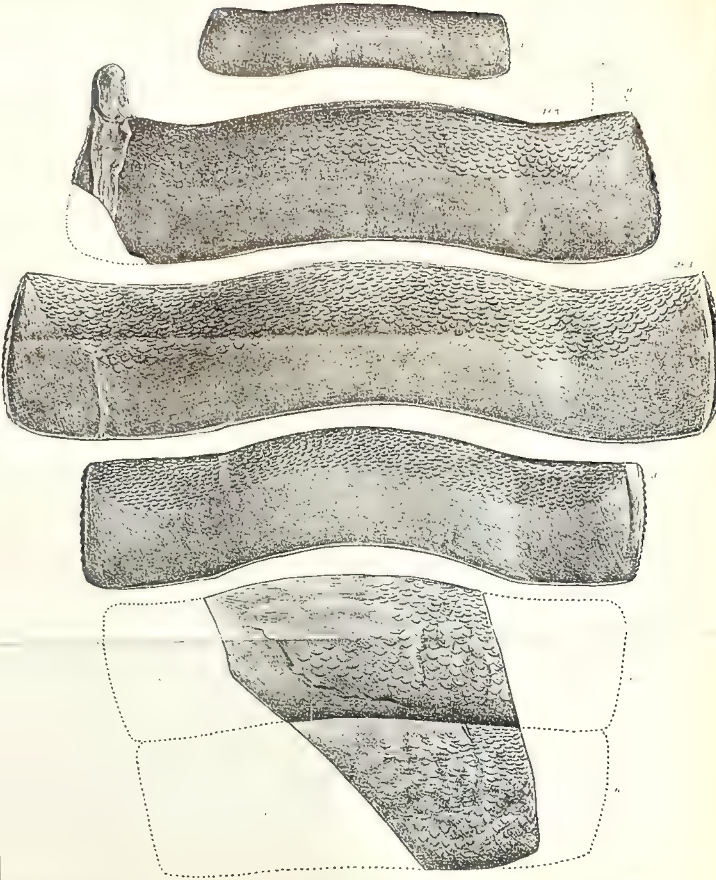
Fig. 2. From the slight obliquity of the lateral edges, this is probably the fourth segment. It is the largest segment of this species known. Reduced to two-thirds. (Lord Kinnaird's cabinet.)

Fig. 3. The fifth segment, the ends almost square. (Collection of the Watt Institution, Dundee.)

Fig. 4. The same segment in a young specimen. (Lord Kinnaird's cabinet.)

Figs. 5, 6. Probably the under surface of the eighth and ninth segments (see Woodcut 9). The posterior segments are more extensively sculptured than the anterior ones, especially on the under side. (Lord Kinnaird's cabinet.)

From Balruddery Den, Perthshire, in the Basement Beds of the Old Red Sandstone.



PTERYGOTUS ANGLICUS

PLATE V. [Plate 16.]

Section 2.—*PTERYGOTUS.*

Pterygotus anglicus. Posterior Body Segments.

Fig. 1. Probably the under side of the tenth segment. It is much narrower in proportion to its length than the anterior segments. (Lord Kinnaird's cabinet.)

Fig. 2. Oblique view of a ring distorted by pressure in a longitudinal direction.

Fig. 3a. A tergal view of the eleventh or penultimate segment, showing its continuous central keel. (Lord Kinnaird's cabinet.)

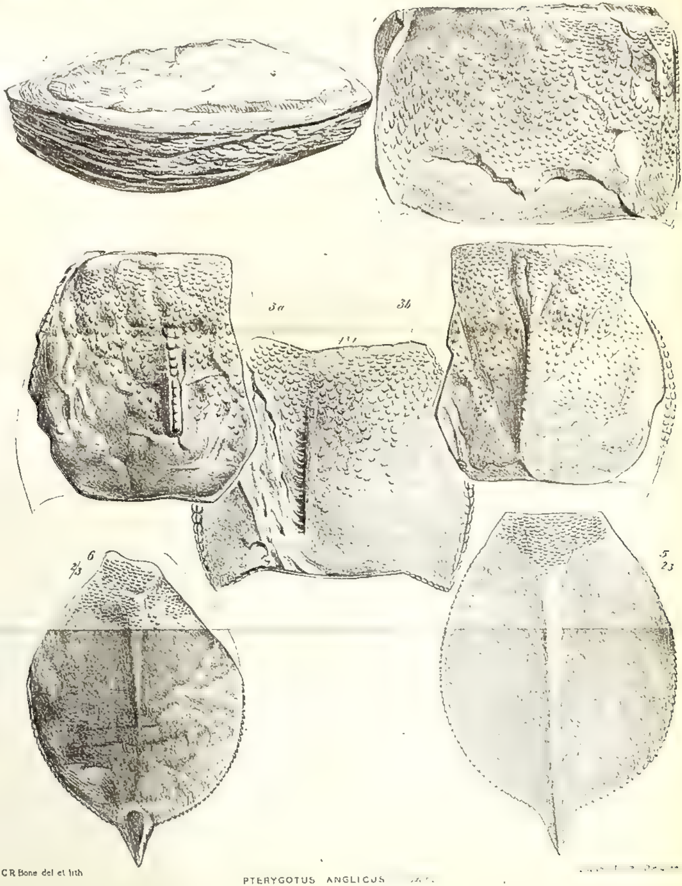
Fig. 3b. Sternal or ventral view of the same specimen, showing a short central ornamented (anal ?) keel. The specimen is much compressed, but is nevertheless convex on both sides.

Fig. 4. An intaglio in sandstone exhibiting the ventral surface of a more perfect specimen; three-fourths of the natural size. (Watt Institution, Dundee.)

Fig. 5. The twelfth segment (telson), tergal side, showing the central keel. (Watt Institution.)

Fig. 6. The sternal surface of a large telson; two-thirds natural size.

All from the Basement Beds of the Old Red Sandstone, Perth and Forfarshire.



C R Bone del et lith

PTERYGOTUS ANGLICUS

PLATE VI. [Plate 17.]

Section 2.—*PTERYGOTUS.*

Pterygotus anglicus. Ectognaths and Antennæ.

Fig. 1. An ectognath or swimming foot, nearly entire ; of the natural size. (Lord Kinnaird's cabinet.) The inner margin and process *a* of the great basal joint *co* are imperfect. The articular process of the second joint *b** (*basignathite*) is broken off from the rest of the joint, *b***, and remains attached to the basal joint. Of the remaining joints, only the impression in the stone of the *upper* surface is preserved. The same letters are applied as in Plate II.

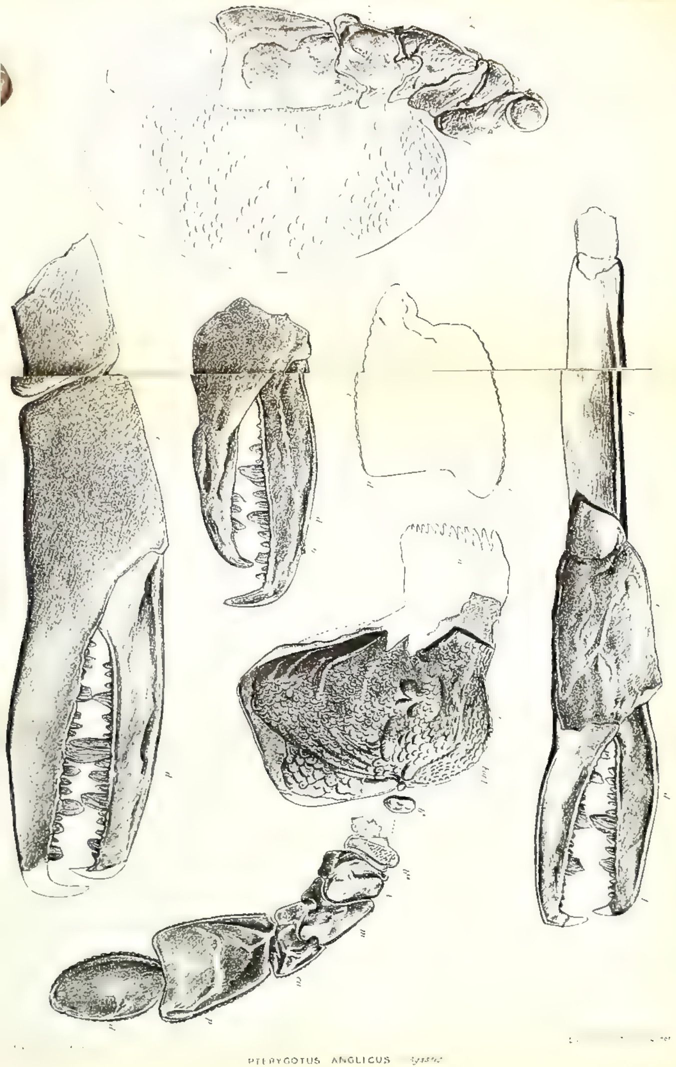
Fig. 2. A larger swimming foot ; reduced to three-fourths its length. Lower and more convex surface of the limb. (Lord Kinnaird's cabinet.)

Fig. 3. The penultimate (sixth) joint of a still larger ectognath or swimming foot. (Same cabinet.)

Fig. 4. An antenna. The articulation between *a* and *b* is not so distinct as it appears to be in the figure ; *c*, the large, swelled, penultimate joint, produced into the fixed ramus of the chela. Usually this branch of the chela is the longer.

Fig. 5. An antenna ; the largest known. (Lord Kinnaird's cabinet.)

Fig. 6. The terminal joints of an antenna, the chela having a very short fixed ramus. (Watt Institution, Dundee.)



PTERYGOTUS ANGLICUS

[PLATE VII. Plate 18.]

Section 2.—*PTERYGOTUS.*

Pterygotus anglicus. Ectognaths and Endognaths.

Figs. 1, 2. The basal joints or coxognathites of the two large swimming feet (or ectognaths). At *c* is the notch for the attachment of the other joints. The pair are probably not placed quite in the natural position, as their expanded bases should be nearer together (after the manner of those in Plate I. fig. 4.) Fig. 1 is of the natural size, and Fig. 2 is reduced to two-thirds its size, to correspond with it. (Lord Kinnaird's cabinet.)

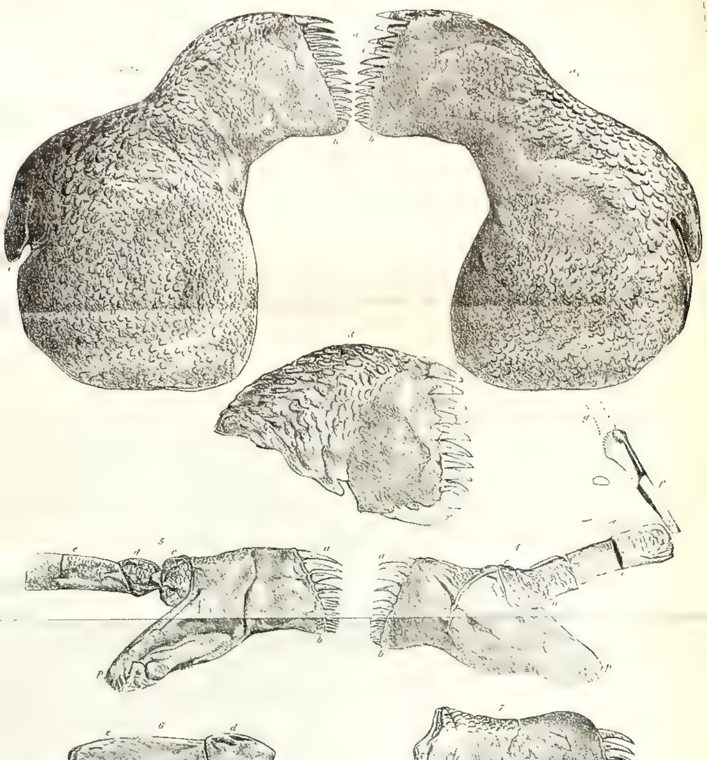
Fig. 3. The end of the serrated process of a large specimen of the same part, which has already been figured by Prof. Agassiz. (Watt Institution.)

Fig. 4. The (right?) endognath, with its long palpus; *p*, the produced outer angle of the basal joint. The terminal joint of the palp *g*, represented in Prof. Agassiz's figure, is wanting in this specimen. (Lord Kinnaird's cabinet.)

Fig. 5. An endognath of the opposite side, with the three first joints of its palpus. (Watt Institution.)

6. The second and third joints of a large palpus. (Lord Kinnaird's cabinet.)

Fig. 7. The basal joint of a much elongated endognath. The region on the inner side of the palpus is much longer than in those represented in Figures 4 and 5, and it probably belongs to a different pair, pp. 187, 248. (Watt Institution.)



C.R. Bone del et lith

PTERYGOTUS ANGLICUS

PLATE VIII. [Plate 19.]

Section 2.—*PTERYGOTUS.*

Pterygotus gigas. Carapace and Body Rings.

Fig. 1. A carapace, imperfect posteriorly.

Fig. 2. The epistoma and labrum ; *a*, anterior broken margin ; the letter *b* is placed near the postero-internal angle of the right lateral ala or lobe ; *c*, the sagittate base of the central lobe.

Fig. 3. One of the thoracic segments. The plicæ are less curved than in the hinder segments,—at *a*, the anterior sub-concave border is visible.

Fig. 4. Another, probably thoracic, anterior segment.

Fig. 5. Sternal view of a segment, showing the anterior articular border and acute margins. The plicæ cover a larger space, and are more pointed, on the sternal than on the tergal surface.

Fig. 6. Apparently the sternal surface of the penultimate or eleventh segment, with the short anal ridge *a*.

Fig. 7. Tergal surface of same specimen. The plicæ cover nearly the whole of its surface.

Fig. 8. Part of the sternal surface of another specimen.

Fig. 9. The sternal surface of the left posterior angle of another specimen. Fig. 9 *a*. The pointed plicæ magnified.

From the Downton Sandstone of Kington, Herefordshire ; in the cabinet of R. Banks, Esq., of that place.

PTERYGOTUS GIGAS

PLATE IX. [PLATE 20.]

SECTION 2.—*PTERYGOTUS.*

Pterygotus gigas. APPENDAGES, &c.

Fig. 1. The swelled base of the antennary chela; two-thirds of the natural size.

Fig. 2. Another specimen, showing the crowded teeth.

Fig. 3. The free ramus of a chela, with the great serrated tooth, *c*; the smaller primary teeth, *b*; and the secondaries, *a*. (*See* Plate XII. Fig. 9*.)

Fig. 4. Part of the serrated lobe of the ectognath.

Fig. 5. Four joints from the proximal end of an endognathary palpus, shortened by pressure.

Fig. 6. The third joint of an endognathary palpus, showing its bilobed distal end.

Fig. 7. The fourth (?) joint, exhibiting its crested distal termination.

Fig. 8. The basal lobe of an ectognath, the serrated lobe imperfect.

Fig. 9. Part of the serrated process of a larger specimen.

Figs. 10 and 12. Joints of the ectognath or swimming foot. 12. The fourth and fifth joints, with part of the penultimate joint, *p**. 10. Penultimate joint, *p**, imperfect.

Fig. 11 is the distal trilobed end of the penultimate joint.

Fig. 13. Anterior end of the sternal surface of the metastoma or post-oral plate.

Fig. 14. Problematical bodies, frequently occurring with this species. The surface when perfect is tessellated as at *a*, but not regularly so.

Fig. 15. Sternal surface of the eleventh segment of the body. The short anal (?) ridge at *a*. Two-thirds of the natural size.

Fig. 15a. Tergal surface of the same segment (compare with Plate VIII. Fig. 7), reduced to two-thirds of the natural size.

Fig. 16. A large caudal joint (telson) with its median crest, seen in profile at 16*c*. A portion of the crest, distorted, is shown at 16*a*, and Fig. 16 *b* exhibits a restoration of its original form.

Fig. 17. One half of the sternal surface of another telson. (Mr. Lightbody's collection.)

Fig. 18. A telson (possibly of *P. ludensis*); two-thirds of the natural size. From the base of the Old Red Sandstone, Ludlow Railway. (Museum of Practical Geology.)

The above, except Fig. 18, are from the Downton Sandstone (Upper Ludlow Rock) at Kington, Herefordshire, and all are in Mr. Richard Banks' cabinet, unless it be otherwise stated.

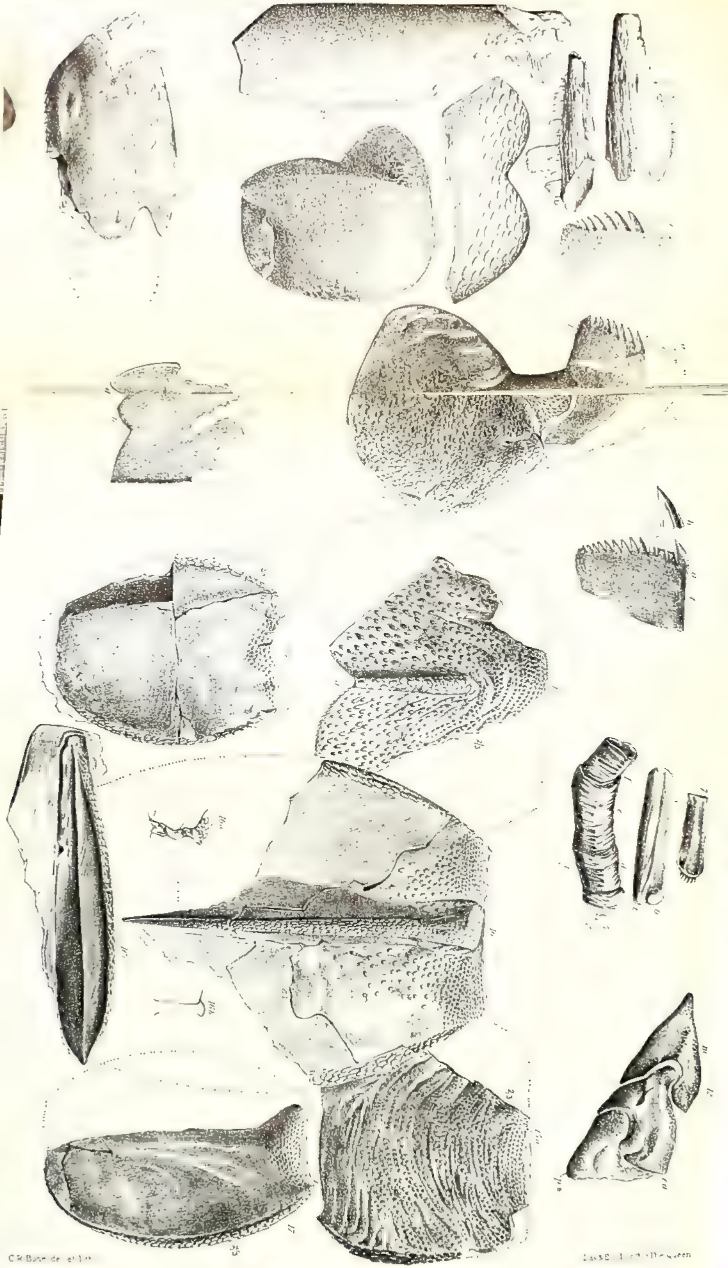


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FIG. 1–17. PTERYGOTUS GIGAS Salter. & P. LUDENSIS

PLATE X. [Plate 21.]

Section 2.—*PTERYGOTUS.*

Pterygotus punctatus. Body Segments, &c.

Fig. 1. The central lobe of an epistoma. (Mr. A. Marston's cabinet.)

Fig. 2. Outer portion of the first segment of the body. (Cabinet of Mr. Charles Weston.) 2 *a*, the margin and the tubercular plicæ of the surface magnified.

Fig. 3. Second segment of the body of a very young specimen. (Museum of Practical Geology.)

Fig. 4. Third or fourth segment. (Museum of Practical Geology.)

Fig. 5. One of the posterior segments, probably the tenth. (Mr. A. Marston's cabinet.)

Fig. 6. The sculpture of this segment, magnified.

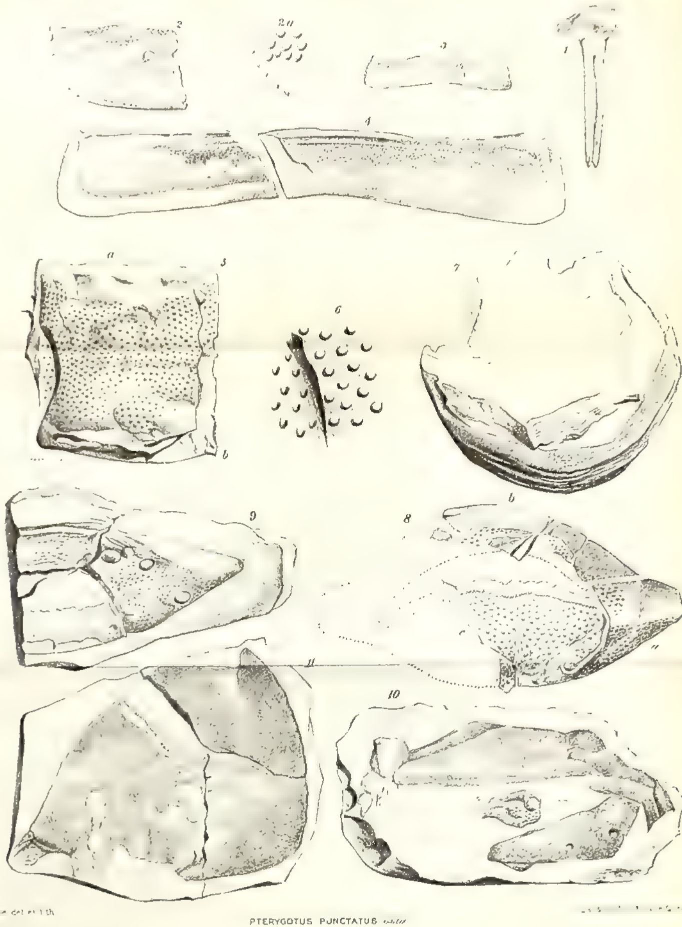
Fig. 7. A segment of the body, compressed longitudinally. (Museum of Practical Geology.)

Fig. 8. A segment of the body (probably exuviated, see p. 257); *a*, lateral sharp angle; *b*, upper surface; *c*, impression of under surface. (Cabinet of Col. Colvin, Leintwardine.)

Fig. 9. A similar fragment (Museum of Practical Geology.)

Figs. 10, 11. Indeterminable fragments. Fig. 11 may be some portion of the telson; it is in Mr. Lightbody's cabinet.

All from the Lower Ludlow Rock of Leintwardine, Shropshire.



PTERYGOTUS PUNCTATUS

PLATE XI. [Plate 22.]

Section 2.—*PTERYGOTUS.*

Pterygotus punctatus. Appendages.

Fig. 1. The fixed ramus of the antennary chela. (Col. Colvin's cabinet.)

Fig. 2. A more perfect specimen, tuberculated at the distal end *a*. (Mr. G. Cocking's cabinet.)

Fig. 3. The terminal portion of one of the rami of a larger chela.

Fig. 4. A metastoma or post-oral plate. (Mr. A. Marston's cabinet.)

Fig. 5. An endognath with its palpus (*a*, *b*, *c*, *f*,) and a crushed ectognath or swimming foot. (Cabinet of Mr. H. Pardoe.)

Fig. 6. An endognath with the proximal portion of its palpus; *a**, the marginal teeth magnified.

Fig. 7. Part of a large endognathary palpus with elongated joints,—the distal and proximal ones are lost.

Fig. 8. The distal end of a large endognathary palpus with short joints, similar to that represented in Fig. 5.

Fig. 9. Four of the curved processes of a large palpus. (Mr. Marston's cabinet.)

Fig. 10. *P. arcuatus.* The basal joint of an ectognath, imperfect posteriorly.

Fig. 11. *P. arcuatus?* The basal joint of one of the endognaths.

Fig. 12. *P. punctatus.* The posterior edge of the basal joint of an ectognath.

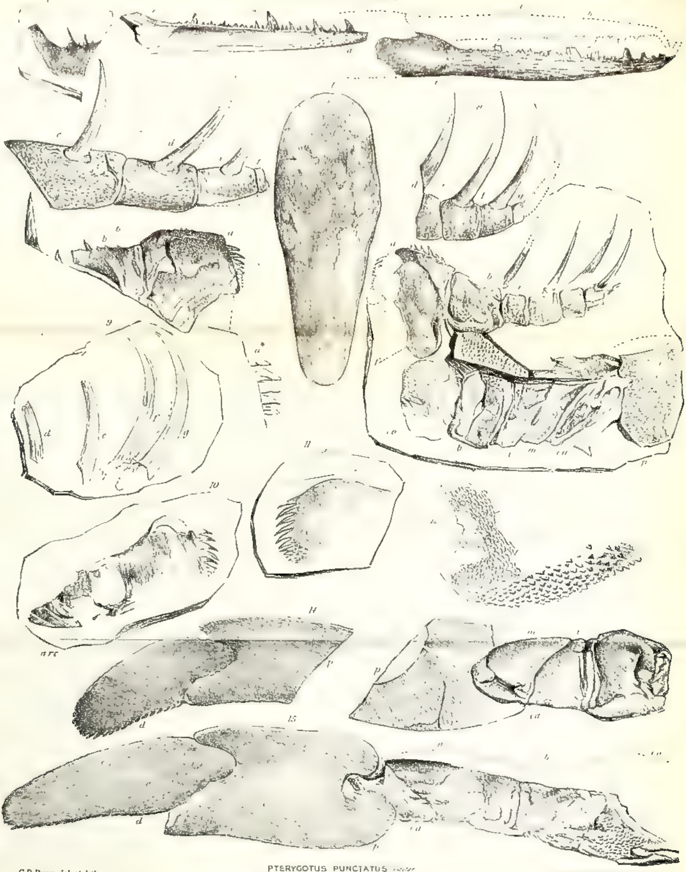
Fig. 13. The second to the fifth joints, and part of the large penultimate joint of an ectognath or swimming foot. (Presented to the Museum of Practical Geology by Mr. R. Lightbody, jun.)

Fig. 14. The end of the penultimate joint, and the terminal palette of an ectognath. (Mr. Marston's cabinet.)

Fig. 15. Ectognath, with the proximal joints more or less injured. The sudden expansion of the two distal joints is clearly seen in this specimen. (Mr. H. Pardoe's cabinet.)

The above are all from the Lower Ludlow Rock of Leintwardine; and, except it be otherwise stated, the specimens are in the Museum of Practical Geology.

(UPPER SILURIAN.)



C R Bone del et lith

PTERYGOTUS PUNCTATUS Salter
(except FIGS. 5 10 11 which probably belong to P. ARCUATUS)

PLATE XII. [Plate 23.]

Section 2.—*PTERYGOTUS.*

Fig. 1. *Pterygotus ludensis.* Fixed ramus of the antennary chela.
Fig. 2. A smaller specimen of the same.
Fig. 3. The metastoma of this species (or possibly of *P. gigas*). 3*a*. The sculpture magnified.
Figs. 4, 5. Imperfect appendages (abdominal ? or thoracic ?). See also Fig. 16.
Fig. 6. The penultimate joint of an ectognath (*P. gigas ?*).

The above are all from the bottom beds of the Old Red Sandstone, or the 'Passage Beds' into the Upper Ludlow Rock, at Ludlow. The following are from the Downton Sandstone, or Upper Ludlow Rock.

Fig. 7. *Pterygotus problematicus.* The fixed ramus of the antennary chela. Whitcliff, Ludlow ?
Fig. 8. The distal end of the same part. Downton Sandstone, Kington. (Mr. Banks' cabinet.)
Fig. 9. A portion of the same ramus of a larger specimen. Upper Ludlow Rock, Ludlow. (Mr. J. Harley's cabinet.)
Fig. 9*. A large serrated tooth, belonging to the (free ?) ramus of a chela. Copied from a figure in the Quart. Geol. Journal, vol. viii. plate 21. Upper Ludlow Rock, Hagley Park, Herefordshire.
Fig. 10. A fragment of a large antennary joint ? U. L. Ludlow. 10*a*. Sculpture magnified.
Fig. 11. The basal joint of an ectognath. U. L. Ludlow. (Mr. Marston's cabinet.)
Fig. 12. The serrated inner lobe of the basal joint of an ectognath (possibly of *P. gigas*). Downton Sandstone, Kington. (Mr. Banks' cabinet.)
Figs. 13, 14. The serrated inner lobe of the basal joint of an ectognath. Fig. 13 from a specimen in Mr. Harley's cabinet ; Fig. 14, from one in that of Mr. G. Cocking. *a*, the small upper tooth.
Fig. 15. A metastoma or post-oral plate.
Fig. 16. An appendage (abdominal ? or thoracic ?), much fractured ; *a*, the slightly mucronate free end ; *b*, the lateral striations ; *c*, a serrated side lobe. (Mr. Lightbody's cabinet.)
Fig. 17, 17a. A similar side lobe, magnified. (Mr. Lightbody's cabinet.)
Figs. 18, 19. *P. punctatus.* Imperfect terminal palettes of the ectognaths. (Mr. Lightbody's cabinet.)
Figs. 20, 21. *P. problematicus.* Anterior and posterior segments of the body. (Mr. J. Harley's cabinet.)

Figures 13 to 21 are from the Upper Ludlow Rock of Ludlow.

Section 1.—*ERETTOPTERUS.*

Fig. 22. *Pterygotus Banksii.* The carapace. From the Passage Beds, at the Ludlow Railway Station. (In Mr. Lightbody's cabinet.)
Fig. 23. The posterior segments of the body, with the telson. From the same locality and cabinet.
Figs. 24–26. Carapaces of different ages. Downton Sandstone, Kington. (Mr. Banks' cabinet.)
Fig. 27. Thoracic segment } From the same formation. (Mr. Banks' cabinet.)
Fig. 28. Abdominal segment }
Fig. 29. The basal joint of an ectognath. From the same formation and cabinet.
Fig. 30. Fixed ramus of the antennary chela. From the same formation and cabinet.
Fig. 31. A metastoma. From the same formation. (Museum of Practical Geology.)
Figs. 32–34. Metastoma. From the same formation. (Mr. Banks' cabinet.)
Fig. 35. The penultimate joint of an ectognath. From the same formation and cabinet.
Figs. 36–38. Telson, of young and full grown specimens. From the same formation and cabinet.
Fig. 39. Carapace of a young specimen. Upper Ludlow Rock, Ludlow. (Mr. Lightbody's cabinet.)
Fig. 40. A portion of an antennary chela. (40*a*, the same magnified.) From the same locality and cabinet.
Fig. 41. A metastoma. From the same locality and cabinet. It is more ornamented than the other specimens.
Fig. 42. *P. Banksii.* The anterior half of the body, exhibiting the carapace, five thoracic segments, and the left ectognath. From the same locality and cabinet.
Fig. 43. One of the thoracic segments (second ?). From the same locality and cabinet.
Fig. 44. A metastoma, exhibiting a mark (indicating its point of attachment ?) at *a*. From the same locality and cabinet.
Fig. 45. The telson. Upper Ludlow, Whitcliffe, Ludlow. (Museum of Practical Geology.)
Fig. 46. The telson (of *P. Banksii ?*) Batchcot, Ludlow. (Museum of Practical Geology.) The shape and striation are different from those usual in this species.

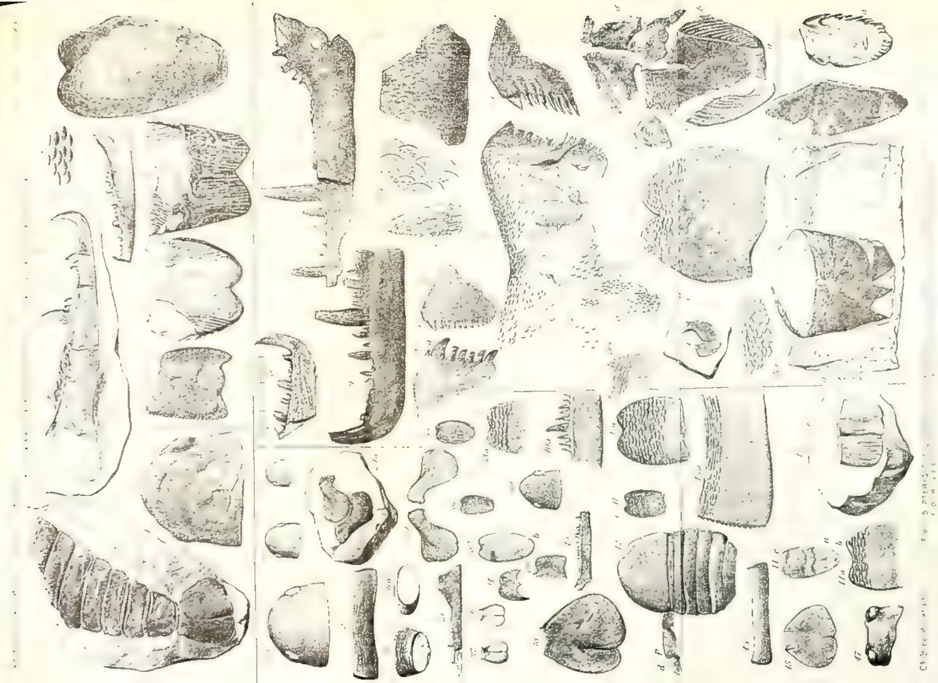


PLATE XIII. [Plate 24.]

Section 2.—*PTERYGOTUS.*

Fig. 1. *Pterygotus acuminatus.* An endognath with part of its palpus.

Fig. 2. An endognath with palpi, from the same slab as the segments of the body figured in Plate II. Fig. 11.

Fig. 2a. The opposite impression of the same specimen.

Fig. 3. Another specimen, with one (or two) endognaths and the proximal divisions of their palpi, covered by part of the ectognath *y*, *x*, (described p. 223).

Fig. 4. A branched palpus, or a pair of palpi (see pp. 187, 223.)

The above are from Upper Ludlow Rock, Lesmahago.

Fig. 5. *Pterygotus punctatus.* Hinder segment of the body? U. L. Ludlow.

Fig. 5a. The plicæ magnified.

Fig. 6. One of the proximal joints of an antenna. 6*a*. The sculpture magnified. From the same locality.

Fig. 7. A portion of a very young antenna. From the same locality.

Fig. 8. *Pterygotus arcuatus.* Part of one ramus of the chela of an antenna, similar to that represented in Plate XII. Fig. 9. U. L. Ludlow. (Mr. J. Harley's cabinet.)

Fig. 9. *Pterygotus punctatus.* A large and perfect endognathary palpus. (Mr. H. Salwey's collection.)

Fig. 10. A portion of one of its curved processes magnified.

Fig. 11. *P. punctatus.* One joint of a very large endognathary palpus, showing the two curved processes. U. L. Ludlow. (Cabinet of Mr. Lightbody.)

Fig. 12. *P. arcuatus.* A large segment of the body (the second). 12*a*. The sculpture magnified. Lower Ludlow, Leintwardine.

Fig. 13. A transverse section of a segment of the body. From the same locality.

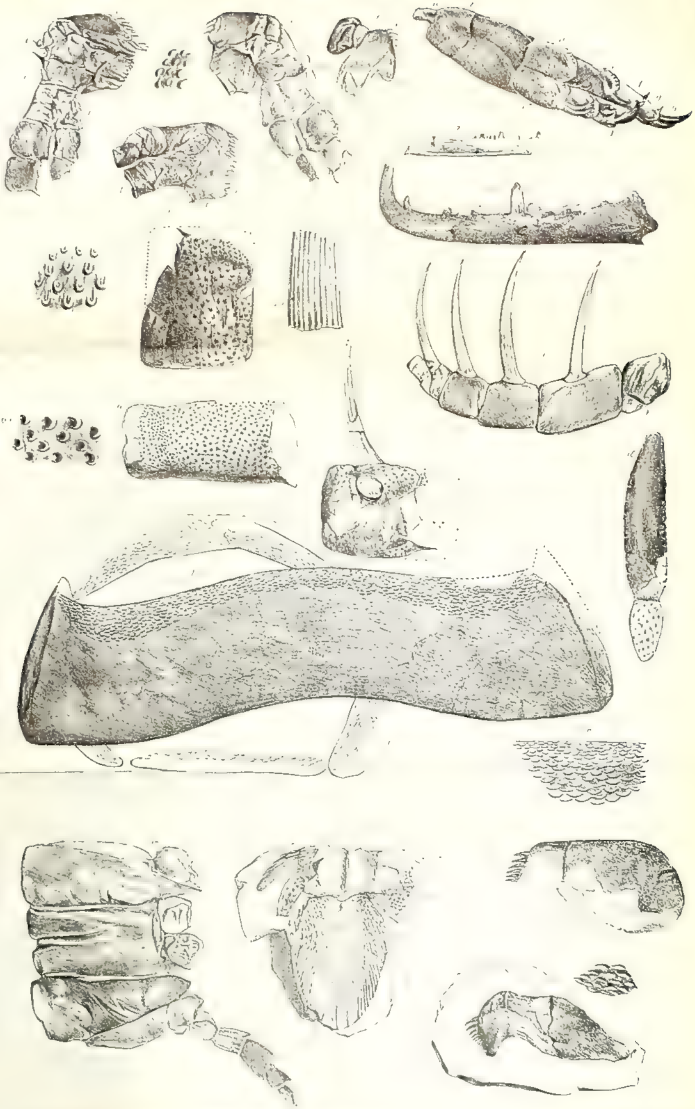
Fig. 14. *P. punctatus.* Part of the basal joint of an ectognath. From the same locality.

Fig. 15. *P. arcuatus?* Part of an endognath. 15*a*. Its sculpture magnified.

Fig. 16. An abdominal? or thoracic? appendage of the same species, showing the incised unequal lobes of the penultimate joint *c*, *d*, and the terminal palette *a*, *b*.

Fig. 17. This figure represents the fossil whose nature is discussed at p. 190. (Mr. H. Salwey's collection.) Lower Ludlow, Leintwardine.

In the Museum of Practical Geology, unless it be otherwise stated.



C.R.Bone del et lith.

PLATE XIV. [Plate 25.]

Section 2.—*PTERYGOTUS.*

Pterygotus ludensis.

Fig. 1. Posterior portion of the body, reduced to two-thirds. 1*a*, the sculpture magnified.

Fig. 2. A fragment of a large segment of the body. (Mr. Lightbody's cabinet.)

Fig. 3. The anterior portion of a segment of the body. (Museum of Practical Geology.)

Fig. 4. The left half of a penultimate segment. (Mr. Lightbody's cabinet.)

Fig. 5. An endognath with its palpus. Fig. 6. The distal end of the third or fourth joint of the palpus. (Museum of Practical Geology.)

Fig. 7. An endognath, probably of a second pair. (Mr. Lightbody's cabinet.)

Fig. 8. The basal joint of an ectognath, with short serrations. (Same cabinet.)

Fig. 9. Part of the inner serrated lobe of a larger specimen. (Same cabinet.)

Fig. 10. The fixed ramus of an antennary chela, with a toothed base. (Same cabinet.)

From the Basement Beds of the Old Red Sandstone. Figs. 1 to 10 are from the Ludlow Railway. Figs. 11 to 13 are from Trimpley, N. of Bewdley, in Mr. G. E. Roberts' collection.

Fig. 11. A portion of a body segment, with prominent plicæ.

Fig. 12. Part of a telson, showing the central ridge, and the radiating lateral lines.

Fig. 13. *Parka decipiens*, Fleming (ovisacs of *Pterygotus ?*) ; the ova remote.

Fig. 13*. *Parka decipiens* in a different state, the ova mutually compressed (see p. 243).

Figs. 14 to 17 are from the Ludlow Railway. Fig. 18 from near the same Passage Beds, the Paper Mill, Ludlow.

Fig. 14. *Pterygotus problematicus ?* A segment of the body ; the plicæ are few and minute.

Fig. 15. A penultimate segment of the same species, showing the short anal (?) ridge on the sternal side. (Mr. Lightbody's cabinet.) Perhaps both Figs. 14 and 15 represent only varieties of *P. ludensis*.

Fig. 16. *P. problematicus.* Part of a large segment of the body. 16*a*. The sculpture magnified.

Fig. 17. A portion of the carapace. 17*a*. The sculpture magnified.

Fig. 18. An undetermined fragment, perhaps a portion of an ectognath. The sculpture is different in different parts of its surface. (Collection of Mr. H. Salwey.)

PLATE XV. [PLATE 26.]

Fig. 1, 1a. *Pterygotus acuminatus*. Appendages surrounding the mouth, but little disturbed (see p. 187). The impressions upon the naturally opposed surfaces of the two portions into which the slab is split are both represented. One-half the natural size. From Lesmahago. (Museum of Practical Geology.)

c, palpi.
c', the toothed edges of the endognaths.
d, the basal joints of the ectognaths; *d'*, their serrated processes.
e, the terminal joints of the ectognathary palp.
g, the metastoma.

Fig. 2. *Pterygotus perornatus*. The carapace and appendages (see pp. 187 and 212); natural size. From Lesmahago. (Museum of Practical Geology.)

b, *b'*, *b''*, *b'''*, the antenna.
c c', endognaths on the right side.
c'', endognath on the left side, reversed in position.
e, terminal joints of ectognathary palp.
g, the metastoma, displaced.
x, palps of the endognaths?

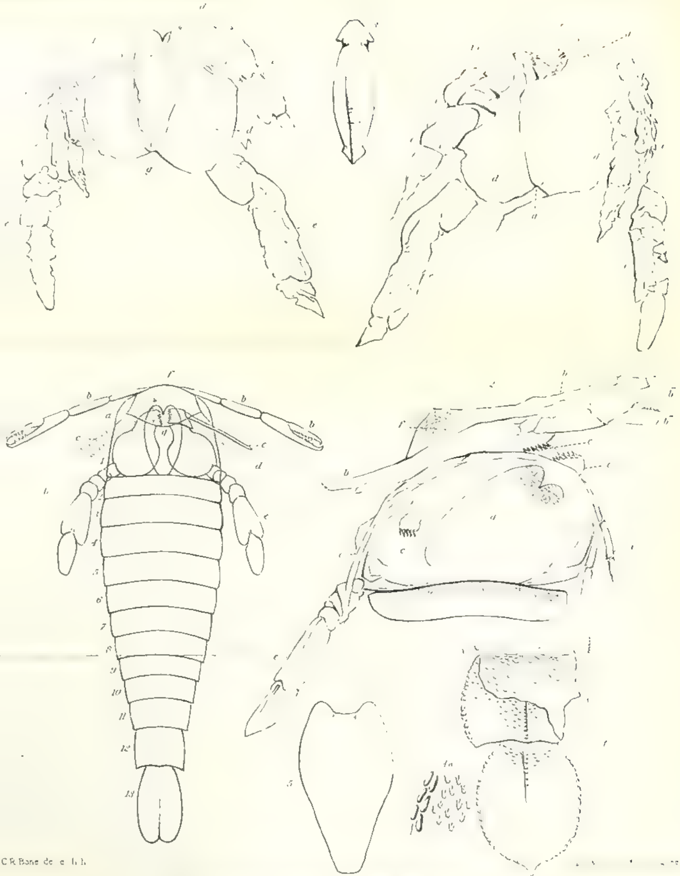
Fig. 3. A problematical fragment; probably the central lobe of an epistomian plate. Lesmahago. (Museum of Practical Geology.)

Fig. 4. *Pterygotus ludensis*. The penultimate segment and telson, of the natural size; 4 *a.*, the sculpture magnified. Base of Old Red Sandstone, Ludlow Railway. (Mr. Lightbody's cabinet.)

Fig. 5. *Pterygotus arcuatus*. The metastoma. Lower Ludlow, Leintwardine. (Museum of Practical Geology.)

Fig. 6. *Pterygotus bilobus*. A restored diagram, of the natural size.

a, eyes.
b, antennæ. *b'*, the chela.
c, the endognaths, with their palps. Their basal joints are, for distinctness' sake, represented as if they were widely separated in the middle line.
d, *e*, the ectognaths, with their palps.
f, the epistoma or conjoined epistoma and labrum.
g, the metastoma.
1 to 13, successive segments; 1, carapace; 2-12, segments of the body; 13, telson.



C R Bone del et lith.

FIG 1 PTERYGOTUS ACUMINATUS. 2 P ...
FIG 4 P LUDENSIS. 5 P ARTUATUS ...

PLATE XVI. [Plate 27.]

Anatomical Illustrations from recent *CRUSTACEA*.

Fig. 1. *Calanus* (spec. ?), magnified about twelve times.

In this and the succeeding Figures the Letters have the same signification.

I′, eyes.
II′, antennules.
III′, antennæ.
IV′, mandibles.
V′, first maxillæ.
VI′, second maxillæ.
lb. ep., conjoined labrum and epistoma.
mt., metastoma.
R., rostrum.
1, 2, 3, 4, 5, 6, thoracic appendages.

Fig. 2. Ventral view of the oral aperture, with the surrounding parts; the palp of the left mandible and the left first maxilla are omitted.

Fig. 3. Right mandible.
Fig. 4. Right first maxilla.
Fig. 5. Right second maxilla.
Fig. 6. First thoracic limb.
} All magnified to the same scale, and the long setæ in all cut short.

Fig. 7. Thoracic swimming limb, the left half only being fully represented.

Fig. 8. *Corycœus laticeps* (?), dorsal view; much magnified.

Fig. 9. Ventral view of the anterior part of the carapace of the same.

Fig. 10. Right mandible of *Nebalia Geoffroyi.*

Fig. 11. Ventral view of the parts about the mouth in a *Pontella.*

Fig. 12. Ventral view of the parts about the mouth in an embryonic lobster (*Homarus*) not yet hatched, showing the large proportional size of the labrum and metastoma.

Fig. 13. Ventral view of the parts about the mouth in *Limulus.*

Figs. 14, Ventral, and 15, dorsal, view of the left posterior thoracic limb, specially modified for swimming, of *Matuta*, a brachyurous Crustacean.*

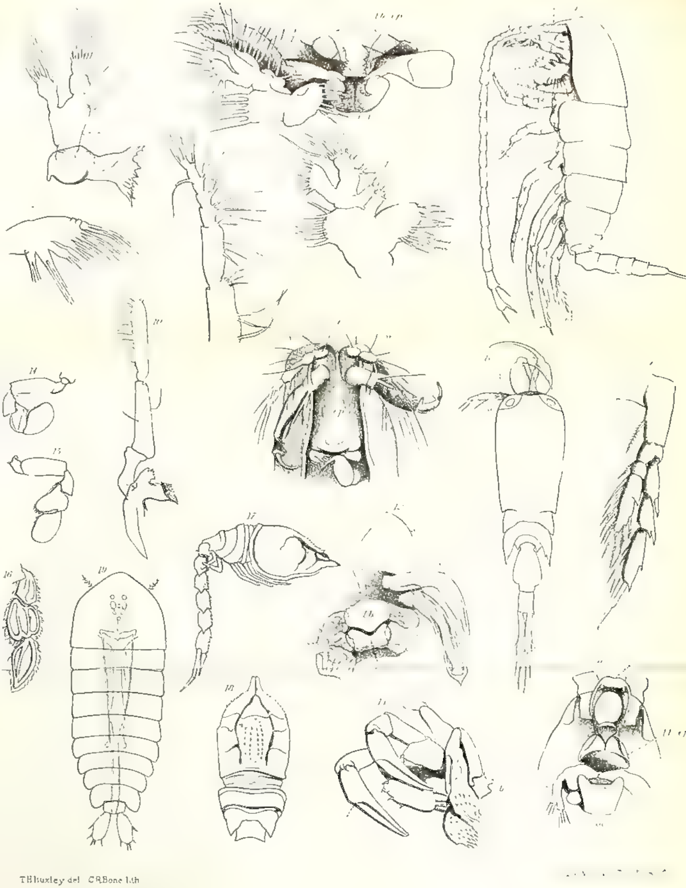
Fig. 16. The corresponding limb of *Portunus puber.*

Figs. 17, 18. Lateral and dorsal views of *Cuma Rathkii*; much magnified.

Fig. 19. *Sapphirina gemma*, after Dana.

* I have added these figures of limbs, specially modified for natation, in some Swimming Crabs, in order to show their similarity to those appendages of *Pterygotus* which served the same purpose.—T. H. H.

Geological Survey of the United Kingdom.



T.H.Huxley del. C.R.Bone lith.

m. (*Merognathite*) rudely trigonal, its hinder base meeting the produced articular lobe of the large penultimate joint *p*.

[Either this or the next joint *ca* bears the long three-jointed filament *t*. The forward salient angle of the limb is formed between this and the succeeding joint.]

ca. (*Carpognathite*) triangular; its convex base outwards, its apex inwards against the process of *p*.

p. (*Prognathite.*) All the preceding joints, except the great basal one, do not quite equal the length of the penultimate joint *p*. It is oblong, but narrower at the base, which is oblique, with the hinder edge produced into a process (*s*), which reaches the fourth joint (*m*). The outer margin is rather convex, the inner a little concave, and the apex deeply and pretty equally bilobed, to receive the terminal joint.

d. (*Dactylognathite.*) A regularly ovate palette, as long, measured along the middle line, as the penultimate joint, and nearly as broad; it is attached to it by a prominent tubercle.

No sculpture has been observed on the limbs.

Metastoma or Post-oral plate, figs. 1, 10.—These cordate plates (referred to the posterior margin of the mouth, p. 182) occur with all the species. The piece is nearly of the same narrow ovate shape in this as in *P. perornatus*, fig. 15, but only one-third the size, deeply cordate, with a sharp notch and rounded lobes in front, and with the base also rounded; the width is about half the length, the lobes are covered thickly with rather large semicircular plicæ, which are absent from the other parts of the plate.

Fig. 1 shows this plate in its natural position, and fig. 10 a detached plate as commonly found. The latter occurs in a group with a pair of antennæ, of which fig. 6 is one, and with the swimming foot, fig. 8; all probably therefore belong to the same individual.

Our specimens are so much altered in shape by pressure, that it is difficult to point out any real variations in form. Fig. 2 appears to have the true general shape. Fig. 1 is evidently compressed laterally, as is the caudal joint, fig. 11; while fig. 12 shows that joint shortened by pressure from behind forwards. Fig. 4 is reduced in length by the same cause, and appears too broad in proportion for the length.

Locality.—UPPERMOST LUDLOW BEDS, Lesmahago, Lanarkshire, with several other species, and the shells *Platyschisma* (*Trochus*) *helicites* and *Lingula cornea.* All in the Museum of Practical Geology. (Collected by Mr. Robert Slimon.)

PLATE I. [PLATE 12] FIGS. 13–15 (AND 16, VARIETY); PLATE XV. [PLATE 26] FIG. 2

P. PERORNATUS.

P. pedalis et ultra, undique squamulis minutis ornatus, capite semi-ovali, thorace segmentis latis curvatis, oculis anticis minoribus granulatis.

SYNONYM. *H. perornatus.* SALTER, in Quart. Geol. Journal, vol. xii. p. 31 and 28, fig. 6.

One of the most distinct and well-marked species, and clearly belonging to the same section with *H. bilobus*, while it is more than double its length and width, the largest specimen being three inches and a half wide and probably not less than fifteen inches in length. We have the head and six body segments ; the swimming feet, both attached and free ; maxillæ with palpi, the post-oral plate *in situ*, with some faint traces of antennæ ; but all these show good characters.

The head (carapace[1]) was formerly described by me as smooth, but in better specimens it is closely and fully sculptured, the plicæ convex *forwards.* It is half a broad oval (fig. 13), three inches in length by three inches in breadth, and the posterior angles are acute.

The eyes are forward and rather small, not extending over a space more than two-fifths the length of the head (in *H. bilobus* they are much more than half), and finely granulated, the lenses visible to the naked eye (fig. 13).

The body segments are broader from front to back than in the last species, the front ones particularly, but, if fig. 16 be the same species, vary considerably in this respect. They are much arched forwards over the wide central portion, the ends are recurved as usual, and at less than one-third from the middle (*b*) a kind of fulcrum exists, dividing the compressed lateral area (pleura) from the more convex central portions. The first segment is much more rounded off at its hinder angles *c* than the remainder, and the space thus left filled by a projecting process of the second segment (see also Plate IV. [Plate 15].) There is a similar but smaller process to

[1] I take leave to use in description the term "head" for convenience sake ; carapace is of course more correct.

the first joint, at least in the var. *plicatissimus*, fig. 16, and it is probably so in all species.

The sculpture in the body rings, fig. 13 *a*, extends over less than half their surface. The plicæ are open forwards, very small, almost linear on the front margin (the extreme margin of all the segments is rounded off and smooth) and the remainder are less than semicircles or they are subangular (more than 90°). On each side at *b* they are not as wide. A transverse impressed line separates the anterior sculptured half from the posterior smooth portion, but this is not always present. No crenate edge has yet been observed.

Appendages, Plate XV. [Plate 26] fig. 2.

On a specimen much distorted, and from which the swimming foot, Plate I. [Plate 12] fig. 13*, is taken, the following organs may be detected by careful examination :—

Epistoma, *f*, reflected from the under side.
Antennæ, *b*, *b′*.
Great post-oral plate or metastoma, *g*.
Two endognaths, *c*, *c′*, with palpi *x*.
Endognath (mandible or maxilla) of the opposite side, *c″*.
A separate jointed palpus.
Ectognath (swimming foot), *e*, attached to the carapace.
First body joint.

f. The large epistomian plate resembles much in shape that seen in Plate I. [Plate 12] fig. 1 *a*, which is similarly displaced. We only see a portion of it, the termination being broken off, but it appears to have been semicircular and semioval, more than three-fourths the width of the carapace, and covered with minute prominent plicæ. Near its base, but not attached, are remains of a single antenna, *b*.

b, *b′*, *Antenna*.—Only the general form can be made out; it is thick in proportion to the size of the specimen, and consists of apparently only three joints, the lower one broken (*b*), the fragment three times as long as wide; the second (*b′*), crossed by a line, which is probably a fracture, appears to be a long single joint, five times as wide as long, its articulation with the neighbouring joints being marked by small irregular crenulations. The penultimate joint or fixed finger *b″* is much crushed, it seems to be contracted at its base, the lower part barrel shaped, about twice as wide as long, and tapering rather gradually into the serrate portion. The

free claw b''' is broad, linear, and beset with numerous small teeth, a few larger striated ones interspersed; the first only is seen on each chela, that on the fixed claw very near the angle; that on the free finger is more distant.[1]

c', c'', *Mandibles*, &c.[2]—There are traces of two pairs of jaws, the palpi attached or in close proximity, figured with the rest of the carapace in Plate XV. [Plate 26] fig. 2. One endognath is lying loose on the left hand of that figure in a reversed position, and has the usual curved striate teeth, but nothing can be determined of its shape. On the opposite side two jaws with palps lie one over the other, and a woodcut is added below, Fig. 2, to show in a diagrammatic form the arrangement of these pieces with their appendages.

The outer jaw *g*, shows the terminal serrate lobe, with at least seven articulated arched teeth (the uppermost largest), and about

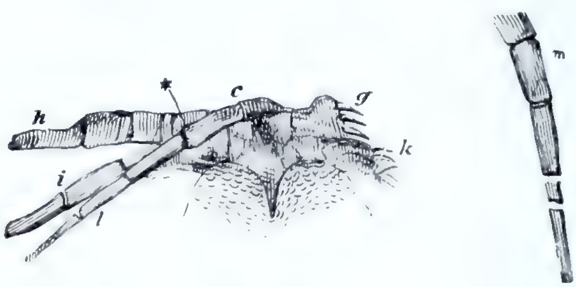


FIG. 2.

Pterygotus perornatus. Mandibles, *g*, *k*; palpi, *c*, *h*, *i*, &c. The post-oral plate is *in situ*. This specimen is the same as that figured in Plate XV. fig. 2, but with some parts omitted.

three times as long as the breadth at their base, and sharp pointed. The other, *k*, is pushed in advance of *g*; it shows a similar set, more displayed, of curved striate teeth; about five are distinctly preserved.

The filament *c*, *l*, which, from analogy with that of *H. bilobus*, is presumed to be the palpus, appears to me to be connected with the mandibular piece *g*, and to cross the two others, *h*, *i*, which seem to form part of a branched palpus, and to belong to a second ectognath (mandible or maxilla). But the connexion of these with the serrated pieces *g* or *k* is not quite certain; they must therefore be described

[1] In *Pterygotus* the large teeth are very nearly opposite one another in the middle and outer portions of the forceps, and must have acted as cutting blades, not merely as prehensile forceps (see Plate VI. [Plate 17].)

[2] Discovered in this species by Professor Huxley. But he does not agree with me, that there is sufficient evidence of the two pairs of jaws, one with a single, the other with a branched palpus (see p. 189).

provisionally as belonging to them. The filament *c*, *l*, consists of at least four elongate sublinear joints, besides a basal one, or probably two, which are short and obscure. The first of the long joints is rather swelled and crenulate or spinose at the tip (at*); the next, which is about four times as long as broad, shows some little crenulation.

Of the branched filament (or pair of filaments) *h*, *i*, the junction with the maxilla is quite obscure; there are about three linear joints to each, broader than those of the palpus, *c*, *l*. The detached fragment *m*, if it belong to this specimen at all, would from its size correspond to one of this pair (*h*, for instance, rather than *l*).

5. *Swimming Feet*, Plate I. [Plate 12] figs. 13*, 14.—Fig. 13* is found attached to the carapace, above described, which has the maxillæ and palpi, &c. attached. Fig. 14 lies loose in the same slab and as it is materially different from that of the other large Lanarkshire species (*P. acuminatus*, Plate II. [Plate 13]), belongs, no doubt, to this. The basal joint (fig. 14) is less expanded in the lower part than in *H. bilobus*. It is rudely trigonal, the sides convex but not equal, the forward edge (14 *a*) being shortest, and the lower angle *d* produced. The neck is rather broad, and the terminal lobe linear-oblong, with a straight serrate edge. The teeth are fourteen, besides the small lower lobe *b*, short and conical, and very obliquely set. The surface is closely plicate (fig. 14 *a*) nearly all over.

The other joints, fig. 13*, are very obscure, but constitute a linear swimming paddle, but little bent, like that of *H. bilobus*. The second joint is lost, but the third (*i*) is linear, the fourth (*m*) triangular, and the fifth (*ca*) irregular and obscure in the specimen. The penultimate joint and terminal palette (*p*, *d*) are much distorted; but in a fine specimen of the carapace, with the swimming feet (ectognaths) attached, and which was discovered by Mr. Slimon since the plates were finished, the penultimate joint (*p*) is more than twice as wide as long, with a strong process from its hinder angle running upwards, and a deeply notched termination to receive the terminal oval palette. This last is short and narrow, compared with that of *P. bilobus*. (See woodcut, fig. 3.) The two ectognaths are very perfect; they are attached at the outer angle, but turned outwards in this specimen by decomposition of the attaching muscles, so that the exterior margins are placed opposite to each other, and the inner serrated lobes look outwards (the dotted lines show what was their original position). The shape of the carapace is distinctly shown in this specimen.

Locality.—Lesmahago, Lanarkshire, with the last. Besides the *Pterygotus acuminatus*, Plate II. [Plate 13], this is the only large species which occurs in the locality. It is not common. Mus. Pract. Geology. (Collected by Mr. R. Slimon.)

P. perornatus, Var. *plicatissimus*, Plate I. [Plate 12] fig. 16.

This, which differs materially in the breadth of the segments, and somewhat also in the manner of sculpture, must be regarded, till

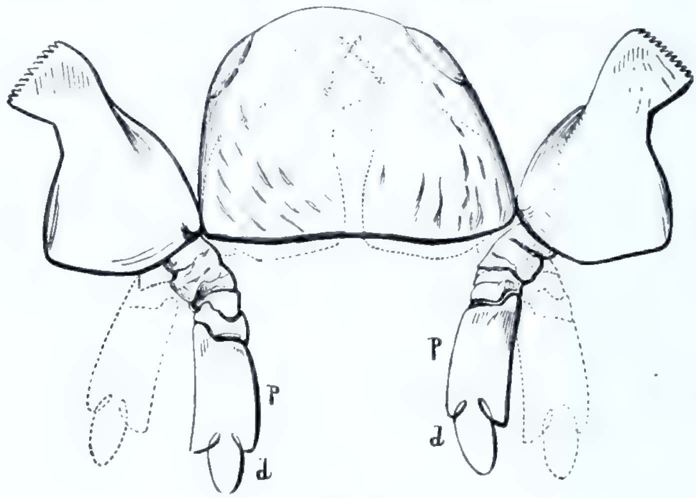


FIG. 3.
P. perornatus, carapace, and swimming feet ; one-third natural size.

more specimens are obtained, only as a variety. But it will very probably be found a distinct species, in which case it is only necessary to use the varietal name as a specific one.

The carapace (in fig. 16) is much compressed longitudinally, but the true form would probably be a full semioval, as in the preceding

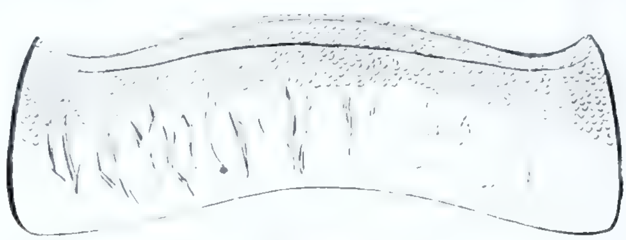


FIG. 4.
Pterygotus perornatus, Var. *plicatissimus* ; 3rd segment. From the specimen figured in Pl. I. fig. 16 ; natural size.

woodcut ; the position of the eyes is obscurely marked. The surface is covered with semicircular plicæ, the curves of which open backwards (contrary to the usual position over the rest of the body).

In front is seen the impression of the large ovate median lobe (*a*)

of the epistoma, shaped as usual, and behind are two radiated muscular impressions (*b*) placed low down on the carapace, and towards the median line, which impressions are probably the attachments of the great swimming feet.

We have only space to figure one of the seven body segments: the anterior six are probably thoracic, the last of these having a large projecting hinder angle which overlaps the base of the seventh (or first abdominal) segment. All the segments are conspicuously broader in proportion than in *H. perornatus*, the second, third, fourth, fifth, instead of nearly five times as wide as long, being not above three and a half times, and this difference is remarkable in the front segment (*c*), which in *H. perornatus* is very transverse, seven times as broad as long, but in this is only four times and three-quarters as wide. It has very distinct anterior lobes, like those of the second segment.

The sculpture of the rings differs from that of *P. perornatus*, in having the plicæ narrower and longer, the angular ones being less than 90°, and even on the anterior margin they are not less than semicircular.

Each segment except the first is crossed by a very distinct impressed line, which bisects the anterior sculptured half, and is placed in the second segment at the anterior third (in the first segment it is absent), the rest have it very near the anterior margin.

The seventh segment is two and a half times as broad as long, and has square, not produced posterior angles.

Locality.—Lesmahago. Mus. Pract. Geology. (Collected by Mr. R. Slimon.)

PLATE XII. [PLATE 23] FIGS. 22-46.

PTERYGOTUS BANKSII.

P. parvulus, 4–5 *uncialis*, *capite convexo*, *semiovali*, *vel parabolico*, *ad frontem subangulato*, *oculis brevibus gibbis*, *ad dimidium capitis : annulis trunci omnibus transversis*, *caudâ expansâ truncatâ bilobâ.*

SYNONYM. *Himantopterus Banksii*, SALTER, Quart. Journ. Geol. Soc. vol. vii. p. 32, also p. 99, and pl. 2, fig. 5 [fig. 6, is the caudal joint of an *Eurypterus*]. Siluria, 2nd ed. p. 266, foss. 66, fig. 1.

Named in honour of Richard Banks, Esq., of Kington, Herefordshire, who has made rich collections of the *Pterygoti* of that locality, and has generously relinquished the publication of his materials in our favour. He has also presented to the Museum all his accurately coloured drawings and notes.

"This small neat species, of which we have many specimens in the Museum of Practical Geology, occurs with *Pterygotus* (*P. gigas*, Plate VIII. [Plate 19]), and spines both of Crustacea and fish, in the yellow tilestone (Downton Sandstone) beds of Kington, Herefordshire. It is there associated with the *Platyschisma helicites* and *Lingula cornea*, Sil. Syst. These are the two species of shells which accompany the fossils of Lesmahago above described, a good argument, therefore, even without other evidence, for regarding these Lesmahago beds as the uppermost portions of the Ludlow rock."—*Quart. Geol. Journ. l. c.*

Description.—The full size must have been from four to five inches long, but the specimens usually met with would probably not be above three or four inches. One or two show the connexion of the body rings with the head and appendages, fig. 42, or with the tail joint (fig. 23). None are quite complete, and though we have nearly all the parts, they are usually disjointed.

The carapace (fig. 22) is a broad semioval, its length as six to seven, except when lengthened or shortened by pressure (figs. 25, 26). It is regularly convex, a little angulated in front, smooth, and bears the small oval eyes rather more than half-way up the head. They are much smaller than in *H. bilobus*, being not above one-fourth the length of the carapace, and very convex.

The body is at first wider than the head and then tapers backwards. The first ring is very narrow (fig. 42), the second twice as broad and with the usual dilated extremities ; the third, fourth, and fifth strap-shaped, arched in the middle and direct on the sides, so that the segment appears much bent. The ends are truncate, in the anterior rings widest behind, and in the posterior ones tapering backwards.

Fig. 28 shows one of the hindermost rings, such as are seen in the more complete specimen, fig. 23. The hinder rings become gradually less transverse, the tenth only two and a half times wider than long, and the penultimate about once and three-quarters its own length.

The caudal joint (telson) figs. 23, 38, 45, differs, in its expanded form, materially from that of *H. bilobus*. It is about three-fourths as long as wide, narrow at the base with two short ridges running down from either angle ; then expanded with somewhat convex sides towards the wide subtruncate apex ; the outer angles are rounded off, the terminal notch shallow, and a short median keel continued from it one-third up the segment.

The sculpture of the head is not known. On the body rings a

transverse lineation running into open plicæ on the sides (fig. 43 *a*) occupies the front margin for not quite half the segment; a few plicæ are intermixed with the lines.

[On the caudal joint, fig. 46, a lineation, parallel to the outer border (*a*), is distinct, but it is uncertain if this specimen be of the same species; it has a strong median groove down the under side, and is less expanded in form than *P. Banksii.*]

The swimming foot, fig. 42, has a characteristic shape, the upper joints (fourth and fifth) are rather narrow, and the penultimate (*p*), instead of being simply conical as in *H. bilobus*, is ovate (more so than in our figure), with the outer border especially convex. It is notched above to receive the fifth joint, and below divided into very unequal lobes. The terminal palette *d* is true oval, rather blunt at its origin and more pointed at the extremity. It is nearly equal to the penultimate joint in length, but considerably narrower.

Fig. 35 is a penultimate joint, probably of the same species.

Antennæ.—Figs. 30 and 40 are presumed to belong to this species, as they occur with them. They are remarkably slender and straight; the base is large and broad, suddenly attenuated into the shaft, which is only a tenth of an inch wide, and three-quarters of an inch long, beset with close small teeth, and furnished with three larger conical ones nearly straight, the central one as long as the width of the shaft. In fig. 40, from the Ludlow Rock, the intermediate teeth are a little longer in proportion.

The basal joints, fig. 29, are flask-shaped, much more elongate in the neck than those of *H. bilobus*, and less swelled at the base. [It is possible they may not belong to the species at all, but to *Eurypterus linearis*, a species which occurs in the same beds; we do not yet know this joint in *Eurypterus.*] The base is subquadrate, quite rectangular on the outer upper margin:—the notch for attachment of the other joints is immediately beneath this angle,—and tapering into the long neck, which has a sharp ridge posteriorly, and together with the terminal lobe equals the length of the basal portion. The teeth are minute.

The post-oral plates, figs. 31 to 34, differ a little in shape from figs. 41 to 44, but not specifically, unless the greater amount of ornament in fig. 41 may be considered sufficient to separate it. The shape is elongate oval, the greatest width at the upper third, the base (*b*) subtruncate, the apex with a shallow obtuse notch. At the lower fourth (*a*) is evidently a tubercle of attachment, and such as occurs in a more linear shape in other species, Plate II. [Plate 13]

fig. 4 *a*. [It is desirable to find out the post-oral plate of *Eurypterus;* which is probably very similar.]

The sculpture is very conspicuous over the upper half; it consists of nearly straight or very slightly curved plicæ arranged in arched lines and ending abruptly against the outer margin. In the sandstone specimens the sculpture does not extend so far down, but it is identical in structure.

Localities.—Upper Ludlow Rock, Ludlow Lane, Whitcliffe (and Batchcot? fig. 46); Parlan, exterior slope of the Woolhope Valley (Mus. P. G.); Kington, Herefordshire (Mr. R. Banks' cabinet). Passage-beds, Ludlow Railway cutting (Cabinets of Messrs. Lightbody and Marston, at Ludlow; Museum Pract. Geol.), &c.

Plate XII. [Plate 23] Fig. 47.

P. Stylops.

P. parvulus, capite (parte anticâ solum asservatâ) 9 *lineas lato, convexo, quadrato, fronte (fracto) producto? lateribus rectis; oculis ad angulos externos fixis, magnis, turgidis.*

This remarkable small carapace, the anterior part of which only is preserved, has occurred to the assiduous search of Mr. R. Banks, of Kington.

Only the anterior part is preserved, and even of this the frontal portion between the eyes is broken off; it was perhaps less prominent than the dotted lines indicate. The forward position and round form of the great eyes very much assimilate the species to *P. acuminatus*, and without doubt it belongs to the same section, or the true *Pterygotus.*

The eyes are remarkably prominent and turgid, a slightly raised fold of the carapace encircling them. A small tubercle, like that on the same part in *P. gigas*, Plate XII. [Plate 23], occurs on the median line of the head, and rather nearer to each eye than their distance from one another. As only a single broken specimen has occurred it is useless to describe it further. There can be no doubt of the distinctness of the species.

Locality.—Kington. (Coll. Mr. R. Banks, of Kington.)

PLATE II. [PLATE 13]; ALSO PLATE XIII. [PLATE 24] FIGS. 1-4; PLATE XV. [PLATE 26] FIG. 1.

SECTION 2.

PTERYGOTUS ACUMINATUS.

P. magnus, 3-pedalis, elongatissimus, capite oblongo angulis quadratis, oculis rotundis minoribus: segmentis corporis 12, quorum quinque anticis transversis bicarinatis, reliquis subquadratis, penultimo oblongo: caudâ ovatâ in apiculum longum productâ.

SYNONYMS. *P. acuminatus*, SALTER, Quart. Geol. Journal, 1855, vol. xii. p. 29, fig. 4. *P. maximus*, id. p. 28, fig. 3. *Slimonia* (1856), D. PAGE, Advanced Text-Book, p. 135, fig. 3.

That the two figures above referred to belong to one and the same species is, I think, almost certain, and all the fragments in our Plate II. [Plate 13], &c., occur in juxtaposition, and are doubtless remains of the same large *Pterygotus*, the finest of the four or five species which were collected from Lesmahago by Mr. R. Slimon. Although not so gigantic as those next to be described, *P. acuminatus* is yet a very large species, and more elongated in all its parts than any of the others. The head is nearly five inches broad and six and a half long, and the seven hinder or abdominal rings, which are different in shape from the anterior thoracic ones, are almost square instead of transverse; while the tail is ovate anteriorly, and behind is drawn out into an apiculus equalling the anterior portion in length.

The Head, Plate II. [Plate 13] fig. 1, is oblong, with straight sides, except at about the anterior third, where it is contracted so as to give it a suburceolate shape; the front is somewhat rounded, and as well as the sides crenated, or rather tuberculated along the edge; the eyes are placed at the anterior angles, as forward as in *P. anglicus*, but much smaller in proportion, oval, about six-tenths of an inch long, and very prominent.

Of the body rings, which are twelve in number, including the tail joint (telson), we have several good specimens. Of these the chief are figs. 10 and 11 in Plate II. [Plate 13]. The former is of the natural size, a young specimen, showing the whole of the body rings; the two hinder ones are left out for want of room in the plate, but these are well seen in fig. 11. The rings are arched, and were probably very convex, and both the front and back edges of the

segments can be seen in our compressed specimen ; the former as a segment of a circle, the latter as its chord.

The lateral hinder edges of at least some of the segments are produced (fig. 10 *g*) into short processes, and their margins are acute.

Six segments appear to be thoracic, and are more transverse than the hinder ones, about three times as wide as long (the front ones still wider), and each is marked at its hinder extremity by two short keels[1] along the median space, not much raised above the surface, and about a quarter of an inch long. The hinder abdominal segments, of which fig. 10 *g* is the first, are destitute of these median keels, and gradually longer in proportion to their breadth till the tail-joint is reached. The first segment (*a*) is only three-quarters of an inch long by one and three-quarters broad ; the second and third (*b*, *c*) are much narrower, about nine-tenths long. The fourth measures more than an inch in length ; the fifth one inch and a quarter, but rather less in breadth, and narrowed posteriorly. It is destitute of any central ridge or keel above or below. The tail segment (telson) in this species is a large oval plate, terminated by a long apiculus ; the length without the apiculus is two inches and a half, and with it four inches ; the breadth is nearly one inch and three-quarters, narrowing to the base, which is thickened, (probably cylindrical,) the rest being much depressed. On the upper surface a strong carina arises near the origin of the joint, and continues to the tip of the apiculus. The lower side is flattened, or but gently convex at the base. The margin of this tail joint is closely serrate or tuberculate in a double line near the base (like that of the margin of the head), running into a single line of distant long tubercles below and along the apiculus.

This kind of double tuberculate border is conspicuous down the sides of the head, the tubercles being elongated, while on the arched front border there are three or four rows.

The ornamentation of the body rings is quite minute, and is but rarely seen in our specimens. It is confined to the anterior border of the segments ; the plicæ are small, equal, and rather prominent.

Appendages.

Antennæ, Plate II. [Plate 13] figs. 2, 3.—The position of these serrated organs is settled by their mode of occurrence in the species previously described. The fragments, figs. 2, 3, being the largest

[1] The first pair is seen in fig. 10, pushed back over the second, and is the best indication of the boundary of the segment *a*.

chelæ in the stratum, and, occurring also with this large species, probably belong to it. The teeth are narrow, lanceolate, shorter than the width of the shaft, turned a little backward, and closely striate. The three primaries are rather more than their own length apart, and the last rather more remote from the terminal tooth, which is curved upwards nearly at a right angle. The secondary teeth are sharp-conical, and five or six in each interspace. The shaft is rather broad, its outer edge quite straight, and at the tip, which is blunt and abrupt, strongly punctured for a short distance. The free claw, fig. 2, has the usual contraction at its base.

Oral Appendages.—From a number of fine specimens from Lesmahago, found since the plates were engraved, some excellent additions have been made to this species; these will be given in woodcuts. They render, I think, unnecessary some of the arguments used further on to prove the existence of two pairs of jaws with their palpi, but as those refer to the evidence as it stands in the plates, it is thought better to retain them.

Epistoma, and labrum.—A piece answering to the shape of this organ in another species (see Plate III. [Plate 14] figs. 2, 5), and of size suitable to that of *P. acuminatus*, occurs with it at Lesmahago. It is specifically different in the great length of the central lobe (*b*) which projects forward a long way beyond the side lobes or wings;

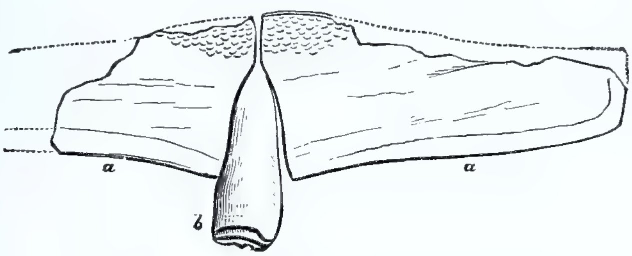


Fig. 5.
Epistome of *P. acuminatus*; half the natural size.

or we may consider these latter as contracted (*a*). The whole piece is transverse, instead of rudely triangular, and the sculpture confined to the anterior border. The median lobe (*b*) is pyramidal, not sagittate, at the base; its tip is broken off.

The occurrence of this more perfect specimen renders it unnecessary to suppose that Plate XV. [Plate 26] fig. 3, should represent the central lobe of this organ. Nevertheless, it has the expanded sagittate base usual in this section of the genus, and from this base extends a narrow lanceolate piece, ridged along the centre, and shelving (to pass under the lateral lobes) on the sides. These contract

near the tip, which is again expanded a little and then forms a cordate pointed lobe. The piece is one inch and three-quarters long, and half an inch wide at its broadest part (below the middle). I do not know to what species it can be referred.

There is yet a third and very large plate found in the same stratum, which, from its shape and structure, appears likely to belong to an allied species, and differs from both the above described. A woodcut (fig. 6) is here given of it, half the natural length. It is keeled along the middle, and rounded near the tip.

Post-oral Plate (Metastoma), Plate II. [Plate 13] fig. 4.—This plate is seen *in situ* (Plate XV. [Plate 26] fig. 1, *g*), and sometimes occurs of large size, above three inches long. The form is broad-

Fig. 6.

Portion of Epistoma. *P. acuminatus* (?) Lesmahago.

linear above, then contracted at the lower fourth to half the width; this lower portion also has parallel sides, is rounded below, and furnished with a strong central keel, which is probably the line of its attachment to the head. The upper end is deeply bilobed, the lobes elliptical, and the notch very narrow; except the raised keel along the hinder portion the entire plate is flat, the upper portion marked with large and rather obscure semicircular plicæ, which are seen occasionally scattered over all the plate. The elongated form of this organ, compared with that of the preceding species, corresponds with the longer shape of the head; and it may, perhaps, guide in determining what the form of the carapace of other species was, where only the metastoma is preserved (as in *P. punctatus*, Plates VIII., IX. [Plates 19, 20]).

Endognaths (*Mandibles, &c.*), Plate XIII. [Plate 24] figs. 1–4, Plate XV. [Plate 26] fig. 1. — These were omitted by accident from Plate II. [Plate 13], but are very important for understanding the structure of *Pterygotus*, since they appear to indicate that the animal possessed two pairs of masticating organs (exclusive of the serrate bases of the swimming feet) as before indicated for *P. perornatus*.

Fig. 1 in Plate XIII. [Plate 24] occurs with the fragments of the species, and probably belongs to it, as its form is so elongated or compressed laterally (compared with those figured on Plate VII. [Plate 18], which belong to a broad-headed species). The length from the serrate edge *a b*, to the end of the basal process *f*, is no greater than the breadth of the serrate margin *a b*. The general form is broad-falcate, the produced base *f* squareish, and the insertion of the palpus *c* very near the serrate margin. This is beset with curved narrow teeth, six or seven of which are distinct in the upper half, and there are numerous smaller ones below. The teeth are articulated with the margin, not mere processes of it, as in the serrate base of the ectognath.

Figs. 2, 3, 4, however, belong certainly[1] to *P. acuminatus*. Fig. 3 shows the endognath *a*, seen only in part with a simple palpus attached *c d*, of which only two joints are preserved; the lowest *c* broad and almost urceolate (not shortened, as in Plate VII. [Plate 18] fig 9), and about as long as wide. The second *d* is narrower; minute plicæ cover the base of both joints. Beneath this, and apparently attached to a distinct plate *e*, pressed closely upon *a*, and sculptured like it, is another and broader palp, of which only the basal joint is visible; and we must refer to a more perfect specimen (fig. 2, 2 *a*) for other details of this appendage.

In fig. 2 the endognath *a* is seen to have a straight edge above with which the serrate margin forms an obtuse angle (about 120°). It is rather suddenly contracted where the teeth begin; they are very oblique, narrow, conical, with a rounded base, and straighter than those of the separate specimen, fig. 1 (the latter is, however, as before said, probably the same species).

The first two joints of the single palpus *c d* are quite distinct, and *c* in fig. 2 *a* shows a toothed distal edge, such as is seen in the joints of fig. 4. The second palpus (probably attached to the crushed second maxillary piece) shows obscurely three or perhaps four broad joints at base *f g*, and then divides into a pair of jointed styles, *h i k l*, with tubercular or spinose joints.

Fig. 4 explains this second appendage, it has a broken and obscure basal portion *a* (which may be part of the serrate basal joint?) followed by three broad joints *b c d*, the second (*b*), being transverse, *c* and *d* are nearly square, thickened at their ends, which are ornamented by a crest of spiniferous tubercles. Similar tubercles

[1] As Prof. Huxley has described Plate XV. [Plate 26] fig. 1, in detail, I need only refer to it here (see p. 188.) It shows, I think, the single and branched palpi; but only one mandibular piece, with teeth, is visible on each side.

occur scattered over the surface, and particularly on the outer edges and down the middle. They are also in parts ornamented with minute plicæ parallel to their length. It is not quite certain if *c* and *d* are single joints, or two styles parallel to one another and pressed closely together, *d* is probably a pair of joints, as besides the crested spiny edge, it is furnished with a pair of thick curved spines (like those of the succeeding joints) on each half. *e f g* in the longer filament are of less diameter, successively shorter, but still thickened at their ends, and furnished with thick curved spines three or four in number; the terminal joint *h*, *l*, in both filaments is a strong simple curved spine, without a striated surface or any serrations to the border. These terminal joints are not well seen in the large specimen figured in Plate XIV. [Plate 25], but the proximal joints are more perfect.

The position given to the palpus in this plate XIII. [Plate 24] with the spiny crests directed forwards, is in conformity with the position of the much larger spines in *P. punctatus*, fig. 9.

It is difficult to prove the existence of two separate maxillary pieces from any of these specimens (Plate XIII. [Plate 24] fig. 2, affording the best evidence on this point). But it seems pretty clear

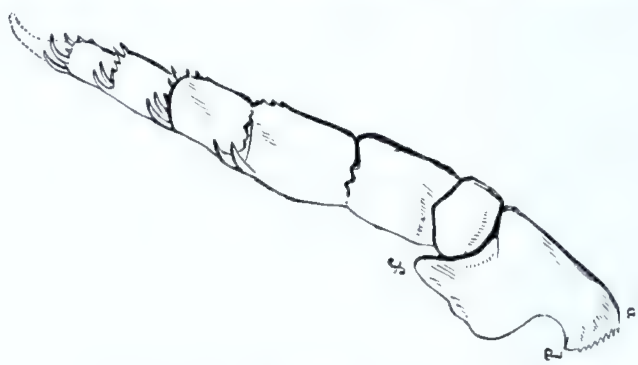


FIG. 7.

P. acuminatus, an endognath with a simple palpus; two-thirds of the natural size. Museum of Practical Geology.

that there were two palpi on each side, one simple, the other branched from near its base:—the number of joints before branching cannot be stated with certainty. If only two filaments be admitted on each side, the alternatives will be—a single mandible with a branched palpus,—or two mandibles each with a simple palpus. We have fortunately met lately with a specimen (fig. 7), tolerably perfect, and showing the basal serrate joint, with six simple joints following; the terminal uncinus is lost. There must, therefore, be two jaws, one of which has a simple palp: the other most probably a branched one.

Lastly, we have a very perfect head of the species, here given, fig. 8, which shows the palps *in situ*, and there is so strong a divergence between the front filament *a*, and the lower one *b*, as to render it probable they are not mere branches of the same palp.

FIG. 8.

P. acuminatus; rather more than one-third natural size. Lesmahago. Mus. Prac. Geol. Specimen showing both first and second pairs of palpi, *a*, *b*, and the swimming foot *c*.

b is far more imperfect than *a*. *c*, is the swimming foot (ectognath) *in situ*.

Swimming Feet, figs. 5 to 9.—The great basal joints of these organs are squarer in outline and their serrate edges placed more vertically (*i.e.* more parallel to the general direction of the plate) than in *P. bilobus* or *P. anglicus*, Plates I., VII. [Plates 12, 18], in order apparently to accommodate their shape to the elongate form of the head. The terminal joints, too, of the limb are less expanded and more linear than in the above-mentioned species.

The size of the largest fragments would give about four inches and a half for the length by two inches and a half broad. The great subquadrate basal joint occupies full two-thirds of the length; it is straight along the inner margin, rather square at the outer and upper angle, rounded on the outer side, and has the notch for the attachment of the remaining joints deep. On the lower third, behind which the breadth lessens, the basal margin is convex. The entire joint is thickened, and most so from the notch obliquely upwards;

a ridge runs along the convexity, and another near the straight inner edge. The terminal serrate portion is narrow-oblong, and set very obliquely on the rhomboidal neck, from which it is obscurely divided. Its upper (forward) margin is strongly arched, and the straight serrate edge furnished with fourteen teeth, besides a prominence on the very small basal lobe. The uppermost tooth is minute, the second largest of all, but not greatly larger than the rest; all are short-conical, tolerably equal in size, and a little curved as well as set obliquely, pointing backwards.

The remaining joints, figs. 7, 8, 9, are well exhibited in three or four specimens, of which fig. 7 shows the impression of the upper side (see for comparison Plate VI. [Plate 17] fig. 1). Figs. 8, 9, are impressions of the lower surface (see fig. 2 of the same plate).

Basignathite.—The second joint *b* is very narrow, almost linear, and fully three times as wide as long; the third (or *ischygnathite*) is linear (?) on the under surface (fig. 8 *i*) but greatly produced forwards on the upper (fig. 7), so as to touch, by its projecting boss, the fifth joint. The general form is rudely trigonal, or rather trapezoidal, the upper straight edge being only about half the breadth of the lower, which is sigmoid, and near the boss tumid.

The fourth joint (*merognathite*) is spherical-triangular before and behind, but on the lower side (fig. 8) it is produced into a long straight process which fits the inner angle of the bend of the limb; a deep notch on the forward edge receives the condyle of the fifth joint. The outer or front margin is very convex, almost gibbous, and forms the prominent forward angle of the foot, which is more strongly bent than in any other species.

The fifth joint (*carpognathite*) is narrow-linear on the upper side, but much broader beneath, about seven lines long by ten or eleven broad, with a rounded boss anteriorly about midway along the joint, and a deep sinus at the hinder edge to admit the great process from the—

Sixth joint (*prognathite*). This is broad-linear, or oblong (the sides straight and parallel), not quite twice as long as broad, exclusive of the lobes above and below. The upper lobe is rounded, fitting into the posterior concavity on the margin of the preceding joint, the lower lobes are unequal, the hindermost being largest and most pointed, the forward one rounded and shorter, the notch deep, rather wide and straight edged at the point of attachment of the last joint (*d*).

(*d.*) (*Dactylognathite.*) This is two and a half times as wide as long, contracted at the base, widest above its middle part, and end-

ing in a blunt point. The margin of this and the preceding joint are minutely serrate.

Locality. — Lesmahago, an abundant species. (Collected by Mr. R. Slimon.) The specimens are all in the Museum of Practical Geology.

PLATE I. [PLATE 12] FIG. 17.

EURYPTERUS LANCEOLATUS.

GEN. CHAR.[1] EURYPTERUS, *Dekay*, 1826. Body as in *Pterygotus, with* 12 segments, eyes subcentral, antennæ without chelæ.

E. elongatus, postice attenuatus, articulis 12, *quorum* 10 *transversis, penultimo oblongo ; caudâ acutâ productâ, ad basin tumidâ.*

SYNONYM. *Himantopterus lanceolatus*, SALTER, in Quart. Journ. Geol. Soc., l. c., p. 28, fig. 5 (*tail joint*).

Perfect, except the carapace, which, when the plate was engraved, was supposed to have resembled that of *P. acuminatus.* It is, however, almost certainly an *Eurypterus*, from the elongate-linear caudal joint, but the shape of the swimming feet is more linear than usual in the genus. It is here figured because of its association with the *Pterygoti* in my former notice.

Body two and a half inches long, by three-quarters wide in the broadest part, which is about the fourth segment ; from thence it tapers very gradually to the last. The anterior segment is narrow (short), not above one-fifth as long as wide, with its ends recurved ; the next, not much broader, is straight posteriorly. The last thoracic ring (sixth) is three and a half times as wide as long, with the posterior angles a little produced ; from thence the joints are larger and less transverse, the tenth being only half as wide again as long. The penultimate joint is about as long as wide, but narrowed posteriorly.

The terminal joint (telson) is three-quarters of an inch long and only two-tenths wide ; it is regularly conical and acute, has a median keel (apparently tumid at the extreme base) nearly all the way down, and also one along each edge.

[1] For remarks on the generic character of *Eurypterus*, see pp. 200, 204. It differs from *Pterygotus* chiefly in the subcentral eyes, but also by the want of the large chelæ to the antennæ.

It is hoped to illustrate this genus in a future monograph, meanwhile the reader is referred to the Quart. Journ. Geol. Soc., vol. xv., for information on the species.

The sculpture is rather obscure, strong on the anterior half of each segment, and faint over the rest ; the borders are smooth.

Swimming Feet.—These are the only appendages found with the present species ; they resemble those of *Pterygotus bilobus*, and, when laid back, reach the end of the fifth segment. The third joint is very obscure ; the fourth trigonal with the longer side outwards, and but little convex ; the fifth irregular, its produced outer edge overhanging the oblong penultimate joint.

This latter (*d*) is about twice and a half as long as wide rather broadest at the bilobed end, the notch deep ; lobes rather acute, the inner much exceeding the outer in size. Terminal palette ovate, its length (measuring from the notch) equal to the penultimate joint without the lobes. Margins minutely crenate.

Locality.—Lesmahago ; only one specimen known. (Museum of Practical Geology.)

PLATES III. TO VII. [PLATES 14, 18].

PTERYGOTUS ANGLICUS.

SPEC. CHAR. *P. gigas*, 6–8 *?—pedalis, capite transverso, anticè angustiori truncato, segmentis corporis transversis, penultimo percarinato (subtus cariná brevi subcentrali), vix expanso, caudâ ovatâ breviapiculatâ, cariná medianâ paullo elevatâ.*

SYNONYMS. *P. anglicus*, AGASSIZ (1844), Poissons Foss. Vieux Grès Rouge, pl. 1 ; M'COY in LYELL (1855), Elem. Manual, 5th ed. pp. 419, 420 (restored). SALTER in MURCHISON'S Siluria, new edition (1859), foss. 21, fig 1, restored ; Trans. Brit. Assoc. 1856, Rep. Sections, p. 75. *Palæocarcinus alatus* (AGASSIZ olim) *fide* PAGE, in Trans. Brit. Assoc., 1855, vol. xxiv. Rep. Sections, p. 90.

The liberality of Lord Kinnaird and of the officers of the Watt Institution, Dundee, has placed at our disposal a magnificent series of this well-known species, including most of the fragments from which Agassiz drew up his original description. We have also to thank Colonel James, Director of the Ordnance Survey, and Mr. David Page, of Edinburgh, for their kind co-operation.

Until the carapace, Plate III. [Plate 14] fig. 1, was obtained, no very complete notion could be formed of the probable size of the fossil. It was a less elongated species than *P. acuminatus*, but taking the proportions of the head and the widest body rings as a guide, and comparing these with such species as *P. bilobus*, the

entire length could not have been less than six, and from the size of the epistoma and some other parts probably reached eight feet in length! There are no living Crustacea which can match this in bulk.

And it was apparently of considerable thickness, almost cylindrical; the crust, however, appears to be very thin and paper like, and only thickened where requisite for the attachment of strong muscles, as in the swimming feet; or along the ridges and margins,—the serrated parts of the mouth, &c.

The carapace, now first described from a young specimen, measures six inches and a half long and fully nine inches wide at the broad base, but narrows considerably towards the front, where it is less than five inches and a half broad.

Our figure shows it compressed a little obliquely, but, allowing for this, it is not far from the true shape, and it is probable that not much of the margin is lost on the right-hand side, while enough remains of the other to indicate that the outline was somewhat curved. Two other specimens in Lord Kinnaird's cabinet show the curved outline. The eyes are distinctly visible on each side, and are as large as crown pieces.

The head must have been considerably more convex than at present, since in our flattened specimen it is corrugated all over; it is sub-pyramidal in shape, truncate or but slightly arched in front between the eyes, and concave posteriorly. The side margins (so far as visible) and the front are strongly crenate, but not tubercular; the general surface appears smooth or minutely punctate, but not anywhere marked by plicæ. The eyes occupy the outer angles of the head; they are oval, an inch and a half in the largest diameter, and about an inch broad. The lenses are rather large, about eight rows in one-tenth of an inch, and in this pressed specimen are rhomboidal rather than hexagonal, at least in arrangement; this may be due to pressure only.

The entire head, compared with that of *P. acuminatus*, is broad and short, and much narrowed in front, so as to be intermediate in shape between that square-headed species and the forms with semi-oval carapaces. The eye is much larger in proportion.

Epistoma and Labrum, Plate III. [Plate 14] figs. 2–5 (6?).—This piece, which is the epistoma or under side of the front of the head, occurs in tolerable plenty, and is the portion formerly supposed to be the carapace itself (see p. 171). From a very perfect and large specimen in the British Museum, a reduced figure (fig. 6) is added, which justifies the inference above drawn as to the great size of

the animal. The figured specimen, 2, is the same as that figured by Agassiz, and is nearly three inches from back to front, but we have other specimens which measure four inches and a half long, and were probably sixteen or eighteen inches wide.

The "*seraphim*," as the piece is called, is straight or only sinuous in front, but broadly wedge-shaped behind; its extremities are unknown, unless fig. 6 be the lateral termination on one side. It consists of a central arrow-shaped piece and two widely-expanded wings or lateral lobes which project backwards nearly as far as the shaft or central lobe, forming with it the broad salient angle of the posterior margin. These lobes are not, however, united with the shaft but overlap it with thickened edges on each side, giving it an appearance of contraction in the middle; it is, when detached, a linear piece, somewhat dilated at the base, convex along the median line, deflexed at the sides, and expanding at the base into a broad arrow-headed plate, the point acute, subtending a variable angle (generally about sixty degrees), and reaching nearly to the front. This portion is divided from the general surface by sutures, but not quite separable. The apex of the central lobe is expanded, rounded, and marked with radiating plaits. As in all other parts of the crust the plicæ which closely cover the surface are transverse and but little curved in front, but become semicircular further back, and then semi-ellipses, and even cones, closely tiling over one another. It is this feather-like arrangement, combined with the shape, which must have suggested the term "seraphim." The extreme margin is smooth. The plicæ on the arrow-headed central piece of the labrum follow the same order from before backwards, and become elongate and prominent along the central ridge, forming tessellæ rather than scales.

Body Joints, Plates IV. and V. [Plates 15, 16].—The segments of the thorax and abdomen may easily be arranged in their right order, from comparison with those of the preceding more perfect species. Plate IV. [Plate 15] represents all the anterior segments we had observed when the plates were engraved. But since their completion, a cast (agreeing very nearly with the figures in Plate III. [Plate 14]) of a fine specimen of the anterior body rings, and nearly a foot wide, has been sent up by our correspondent, Mr. W. Miller, of Dundee. It is from a new quarry at Tealing, Forfarshire. The specimen is in the Museum of the Watt Institution, Dundee, and a woodcut, one-fifth the natural size, is given of it in p. 231. From the second to the ninth, the segments are all united, and the anterior ones have slipped a good deal over one another so as not to present quite their full dimensions.

1*st Segment*.—This appears to be wanting both in the Tealing specimen, and in the specimens figured in Plate IV. [Plate 15]. It was, probably, narrower than all the rest and had the outer posterior angle much rounded off.

2*nd Segment* (woodcut, No. 9).—This is five times as wide as long, somewhat arched in the middle, and much bent forward at the

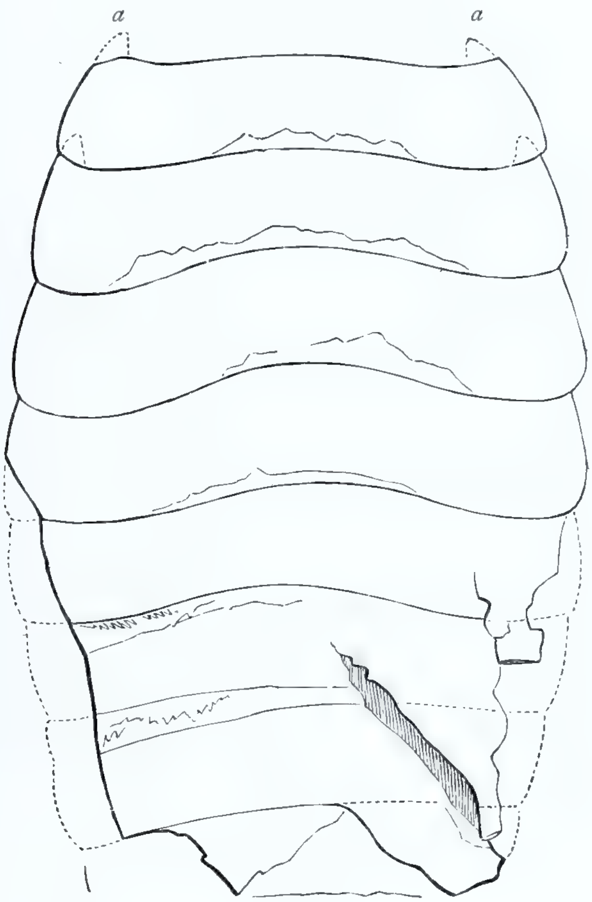


FIG. 9.

Pterygotus anglicus, from the second to the ninth body ring; one-fifth the natural size. Lowest beds of Old Red Sandstone, Tealing, Dundee. This specimen is in the Museum of the Watt Institution, Dundee.

sides, with indications of lateral processes *a*, *a*, similar to those in the third segment. The lateral edges are very oblique: forming an angle of about 70° with the posterior edge.

3*rd Segment*, Plate VI. [Plate 17] fig. 1. — This is Agassiz's figured specimen in his Table A, upper right-hand figure. It is four and a half times as wide as long, our largest specimen above ten inches wide. The posterior angles are rounded off, the anterior

produced into lobes an inch in length, *a a*. The lateral edges are less obliquely truncated than in the second segment.

4*th Segment*.—Wanting in our plate; it is the largest and broadest of all in the Tealing specimen (woodcut 9); its sides are less oblique than in the third segment.

5*th Segment*, Plate IV. [Plate 15] fig. 2.—Fully five times as broad as long, the sides are nearly rectangular, not oblique, the posterior angles very little rounded, the anterior not (?) produced. Our largest specimen measures more than a foot wide and two inches and a half long.

6*th Segment*, Plate IV. [Plate 15] fig. 3.—Of the same shape as the fifth, but only four times as broad as long.

Of the remaining rings, figs. 5, 6 show imperfect fragments. They gradually taper backwards, as indicated by the dotted margins, and become thus narrower in proportion to their length, but exhibit no other difference, as we learn from the above perfect specimens, as far as the ninth.

Plate V. [Plate 16] fig. 1, can scarcely be any but the tenth segment. It is about once and a quarter as wide as long, the sides straight, and the posterior angles a little produced.

The 11*th segment*, figs. 3, 4, suddenly changes shape, it is half oval, with both ends truncate, and its length is rather more than three-fourths of the width. The base is contracted, the sides curve boldly outwards, and again contract at the produced and hooked posterior angles. The segment is thus much broadest behind. We have both upper and under surfaces, the former is carinated all the way down by a strong median ridge, wider and less prominent at first, then sharply elevated and covered with coarse squamæ. The under side, fig. 3 *b*, has no median ridge except for its middle third, and this, which begins by a gentle elevation, ends abruptly rather more than two-thirds down. It is closely covered with large squamæ, and probably indicates the place of the anal opening. The lateral and posterior margins are also bordered with tubercular squamæ, largest and most conspicuous on the sides. Our finest specimen is three inches and three-quarters long, and four inches and a quarter wide behind the middle, where the width is greatest; at its upper end it is only two inches and a quarter broad.

In the same beds, near Forfar, penultimate joints occur, which are probably of the same species, but show a marked difference from those in the plate. An upper and under side is here figured. The former is destitute of any carina; on the latter an abbreviated (anal?) ridge exists, but on the posterior third only (exactly as in

P. gigas, Plate VIII. [Plate 19] figs. 6, 7). The proportions also of these joints are different from that of the corresponding part in Plate V. [Plate 16] figs. 3, 4, being greatly more transverse; two-thirds as long as wide in fig. 1, and about three-fifths in fig. 2. This proportion is not very different from that of *P. gigas*, though the shape is so different. May these not be differences of sex,

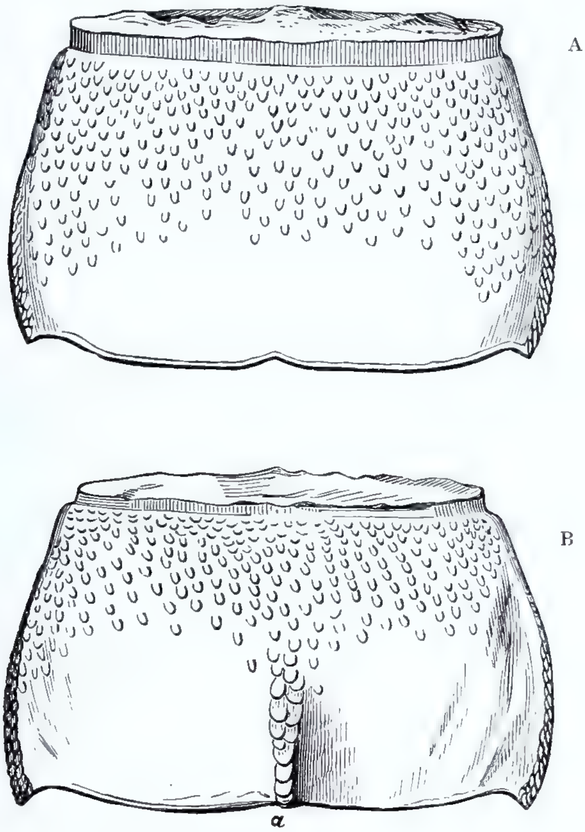


FIG. 10.

Pterygotus Anglicus? or another species. Penultimate body joints, upper and under sides. A the upper side, and B the under, showing the anal ridge *a*. Base of Old Red Sandstone, Leysmill, Forfarshire.

instead of indicating a second species? The ridge (*a*), supposed to be anal, is present in all the species, either subcentrally or on the hinder edge of the segment.

Telson, Plate V. [Plate 16] figs. 5, 6.—The tail joint (12th) is a broad oval, contracted at its base of insertion, widest *posteriorly* below the middle, and shortly apiculate at the tip. It is but little carinate on the dorsal view, fig. 5, and flat or with a very slight median ridge below fig. 6. In a specimen six inches long the apiculus does not project half an inch from the general margin, which is squamate and serrate, but not strongly so. The apiculus itself is not serrated.

Sculpture.

The whole of the body rings are ornamented with a similar sculpture, although not equal in size or distributed exactly in the same way over all the segments. Curved plicæ, like those which occur on the epistoma, occupy the anterior half of each body segment, and are from one to two lines wide, in open semicircular curves upon the middle parts and anterior angles of the segments, but on the front edges they are nearly straight lines and much more crowded.

This arrangement is nearly uniform for the first five or six rings, the plicæ ceasing rather abruptly about the middle of the segment. In the hinder ones they cover a larger surface, Plate V. [Plate 16] fig. 1, and on the under sides of all the segments (Plate IV. [Plate 15] figs. 5, 6), they also occupy nearly all the surface, though more sparingly placed on the posterior half. On the 11th segment, the plicæ reach down along the central keel, but are absent from the outer angles, and on the under side, fig. 3 *a*, they occupy a still smaller area; while on the caudal joint only a small portion near the base or insertion of the joint is marked by them.

In the hinder rings, the tenth and the two last especially, the sculpture on the dorsal side is more angular; the plicæ being longer and narrower than even on the ventral side, where it is usually more angular than on the upper surface. As inattention to this point might mislead in comparing with other species (*P. gigas*, for instance, Plate VIII. [Plate 19]), it is of consequence to note this difference in the ornamentation of different portions.

Appendages.

Antennæ, Plate VI. [Plate 17] figs. 4, 6.—They were of great size. Plate VI. [Plate 17] fig. 5, shows the largest we have seen, but a somewhat smaller size (fig. 4) is not at all unfrequent. There are four joints, including the free terminal claws.

Of the first articulation only short fragments remain, it is narrower than the second, which is linear, scarcely contracted at either end, and in the largest specimen must have been four inches and a half long and one inch and a quarter broad. The penultimate joint, which is produced into the fixed claw of the chela, is rather suddenly swelled, and increases in width outwards to the insertion of the terminal joint. The produced portion is fully four inches long, rather narrowed at its insertion (so as to be a little fusi-

form), and thence tapering to the abruptly curved tip, which bends up at a right angle, and is frequently half an inch long and pointed. The opposed free claw is of the same shape, but more equal in breadth, generally longer, fig. 2, than the other, but sometimes the two are nearly equal (fig. 1). Occasionally the moveable joint is largest, fig. 6, and overhangs the other considerably.

It is difficult to say which was anterior, but from the curvature probably the free joint was forward, as in our figure. Each half of the forceps similarly armed with about four primary and ten or eleven secondary teeth, three or four between each pair of primaries. These are set on at right angles, or rather pointing a little forward on the fixed finger, but on the moveable claw decidedly backwards. They appear to have been much compressed, and were so long that when the chela was closed they shut side by side like the blades of a pair of shears; and they are placed opposite to one another as if for the purpose of cutting as well as seizing. The middle pairs are longest, sometimes measuring half an inch. The pair next outwards from these are nearest in size, and the outermost and innermost pair (when the latter are present) are smallest.

The shape of the large teeth and of many of the smaller is ovato-lanceolate, constructed just above the immediate base, and then expanded into a lancet form, and longitudinally striated, the striæ radiating a little from the base on the forward edge. Some of the smaller teeth are simply conical, and the striation of all is about equally coarse.

Endognaths, Plate VII. [Plate 18] figs. 4 to 7.—There are five or six specimens in the Scotch collections more perfect than that figured by Agassiz (middle left-hand figure), and of larger size, fully four inches and a half long. The palpus, *c d e*, was probably five or six inches in length, and of considerable thickness. Some fragments even indicate a still larger size for the jaw.

The mandible is of an oblong form, the front and back margins nearly parallel. The serrate termination of the lamina scarcely at all expanded into a lobe, and the posterior or basal portion (*p*) which occupies nearly half the entire length is produced obliquely backwards at a wide angle. This portion is straight in front and only slightly sinuous along the hinder edge, which shows traces here and there of striæ perpendicular to the edge, probably due to the insertion of muscular fibres.

The serrate edge is nearly straight and very oblique, forming an angle of about 120° with the front margin. There are about twelve strong teeth, of which the upper six or seven are free, lanceolate,

curved, and dilated below, with a constriction as if articulated, and the remainder are connected so as to form ridges upon a thin plate Minute intermediate ridges occur between these. The posterior angle of the serrate edge is produced a little into a small lobe *b*, covered with deep punctures as if for the insertion of stiff hairs or setæ. The upper edge is not at all expanded or overhanging as in *P. acuminatus*, the teeth starting at once from the upper angle in a line continuous with the front margin (this is not the case with fig. 7, in which there is an overhanging lobe).

The general surface of the mandible is covered with obscure plicæ, which become distinct and large along the front margin, which is thickened ; the rest of the lamina is rather flat, the base is thin and almost membranous at the edge.

The palpus is long and stout, directed straight outwards, and consisting of at least five, and probably more joints, of which the basal one (*c*) is more than twice as wide as long. The next (*d*) unceolate and thickened at the distal end, rather longer than wide. The third takes an elongate form, but is still broad, and its end thickened and somewhat bilobed (*e*). The next (*f*) is still longer in proportion, swelled, and a little crenulate or spiny at the tip (compare with Plate IX. [Plate 20] fig. 7). We have no more joints, but in Agassiz's figure the succeeding joint, the fifth, is clearly shown.

The surfaces of all these joints are covered with transverse plicæ.

Maxilla? fig. 7.—It is probable that fig. 7 indicates a second pair of endognaths, since the proportions of the plate are so different, fig. 7 being considerably longer before the insertion of the palpus than fig. 4, and having an overhanging rounded lobe in front above the insertion of the teeth. Some specimens agreeing with this in proportion have the basal lobe of the palpi broader.

Swimming Feet (*Ectognaths*), Plate VI. [Plate 17] figs. 1 to 3, Plate VII. [Plate 18] figs. 1 to 3.—The large basal joints of these organs are among the most characteristic parts of *Pterygotus*, and were at first supposed to be the mandibles or maxillæ, as they are most frequently found detached from the other joints of the limb. Agassiz figured a portion as a part of the tail flap, and we reproduce his original specimen, Plate VII. [Plate 18] fig. 3. It will be best to describe this portion first. It is the—

Basal Joint (*Coxognathite*), Plate VII. [Plate 18] figs. 1 to 3.—These are six inches and a half and even seven inches long! and not less than three inches broad, gently curved (flask-shaped) convex, with the outer or forward edge thickened, and concave on the inner

or hinder side, with the large basal portion almost orbicular, but narrowing into the neck, and the terminal lobe again somewhat broadened and subrhomboidal, with the serrate border placed obliquely to the general direction of the entire joint.

The teeth are twelve in number, gradually longer from behind forwards, the first often five lines long, and three broad at base. They are conical, a little curved and grooved down the middle, but not at all articulated to the base. Being set on a straight margin and regularly increasing in size forwards, they present a serrate edge along the points, rounded off a little behind into a very small basal lobe *b*. There are the same number of teeth in young as in mature specimens.

Large tubercular plicæ cover the whole surface, except the inner thin margin of the terminal lobe, and these are concave everywhere to the border, except towards the inferior angle behind the attachment of the foot (Plate VII. [Plate 18] fig. 2 *c*), where they present their convex side to the margin ; and hence this portion is easy to identify, even in fragments.

The limb beyond the large basal joint is very suddenly contracted. The point of attachment for these is very conspicuous, as a deep notch in the foliaceous base, about half way up on the outer side, and from this point to the upper angle of the serrate tip is the line of greatest convexity. The basal edge is rounded below, but angular where it joins the inner margin.

The other joints of the limb are represented in Plate VI. [Plate 17] figs. 1, 2 ; and we are able to give a more complete account of them in this than in any other species ; fig. 1 represents the upper and fig. 2 the lower surface of the limb.

b. The second joint (*basignathite*) is transverse, more than twice as wide as long, and furnished anteriorly with a large rounded boss occupying the exterior third of the joint (*see* fig. 2), broken off from the limb and left attached to the coxal segment in fig. 1 at *b**. Its hinder articulating border is somewhat concave, its inferior angle rounded and produced.

i. The following joint is subtrigonal with rounded sides on the upper surface, and with an obtuse angle projecting over the centre of the following joint, but on the under surface it is rhomboidal, more than twice as wide as long, and with the distal and proximal edges nearly parallel (*ischygnathite*).

m. The fourth joint is trigonal, the outer edges wide, convex, and forming the angle of the limb, terminating in a rounded process extending half way down the following joint. On the upper side,

fig. 1, the distal articulating edge is produced; on the under side, fig. 2, deeply emarginate to receive a process from the fifth joint *c a.* The inner side of this joint (*merognathite*), which is rather a difficult one to describe, is much narrowed, and terminates in an acute angle opposed to the wide basis of the outer margin.

c a. Of the next joint (*carpognathite*) it is equally difficult to give a clear idea; its shape is irregular. It is somewhat crescentic on the upper surface, its outer side much the longer, and its distal margin oblique, nearly straight for the greater part of its length, but the outer angle truncated, and the inner notched. On the under side it follows the shape of the preceding joint, and has a prominent median process above to fit into the notch of it. Its distal margin, too, on this surface is sinuous, and less oblique than on the upper side.

p. (and fig. 3). The penultimate joint (*prognathite*) is flattened (to form with the last, *d*, a swimming palette). Our largest specimen measures two and a half inches in length, by one and a half at its broadest part. It is somewhat quadrangular, but one-third broader below than above. Its outer edge is perfectly straight, longer than the inner, and terminating above as a narrow rounded lobe, behind which is a deep emargination, continuous with the curved outline of the inner margin. The latter is produced inferiorly into a subtriangular lobe (3 *c*), broader than the superior process of the outer margin above described. The rest of the inferior border (*d*) is nearly straight, and forms almost a right angle with the straight outer margin.

d. The terminal palette (*dactylognathite*) is broadly ovate, twice as long as broad, its apex rounded, its outer margin quite regular; the inner a little flattened above, leaving room for the play of the palette against the penultimate joint, as in the swimming crabs.

The surface of the great basal joint is nearly covered with large plicæ or squamæ, the convexity of which is outwards over the lower and hinder half, and inwards along the front margin. The other joints are more strongly ornamented, the plicæ coarsest on the exterior margin: on the three or four terminal joints they are only obscurely visible except on the margin.

The margins of at least the two last segments are beautifully crenulated all round, with appressed serratures; these are largest at the apex and inner edge of the terminal swimming palette.

Metastoma, Plate VI. [Plate 17] fig. 7.—The only piece which remains to be described is this large oval plate, deeply notched at the broader anterior extremity, regularly rounded on the sides, and

very slightly truncate at the posterior end. These plates are sometimes four inches long and three broad, and are oval, the greatest width being less than half way from the notched end; flat on one side and of but slight convexity on the other, except at a point on the median line about one-third distant from the smaller end, where there is a prominence (probably the point of insertion). They are more covered with sculpture than in the species previously described.

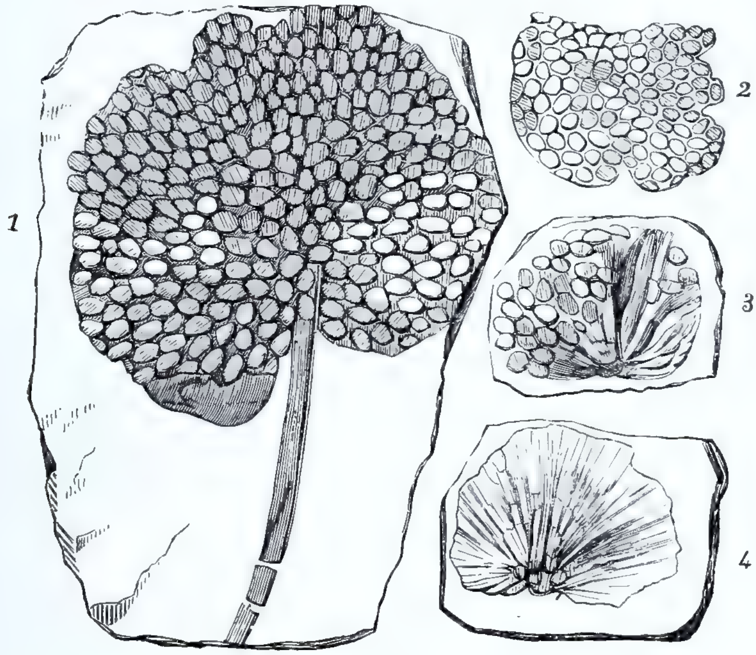


FIG. 11.

Packets of eggs or ovisacs (*Parka decipiens*). No. 1 is from a specimen in the cabinet of Lord Kinnaird.

(*Parka decipiens*, Fleming. See Siluria, 2nd ed. chap. 10.) These occur too often with *Pterygotus* not to be suspected as part of its structure, and are found with the *P. anglicus* in Forfarshire and Perthshire; also, with *P. ludensis* at Kidderminster, and *P. problematicus* at Ludlow.

Four fine specimens lent us by Dr. Balfour, of the Botanic Gardens, Edinburgh, show clearly that the bodies in question cannot be referred to seed vessels or receptacles, or indeed any other portions of a plant. There is no trace of a style on any of the carpels of the supposed fruit, nor of a leafy involucrum below it.

They are rounded masses, one to two inches broad, and composed of numerous oval or hexagonal areæ, a line or two in diameter, which are now flat, but appear as if they had been compressed from a nearly

globular shape, not crowded over each other, but arranged in nearly one plane so as to form a disk.

A long pedicle, fully a line broad, is attached near the centre of the disk so formed, or sometimes nearer its margin; and from the point of attachment the surface of the general enclosing membrane is radiated or plaited to the margin, but only on one side of the disk. The plaits are depressed lines, dichotomising and inosculating a little, but seem to have no reference whatever to the arrangement of the ova, which they cross without being interfered with by them.

The appearances presented would be best explained by the supposition of the fossils having been membranous disks of only a moderate thickness, and containing a single series of ova in the thickness of the disk. They are not superimposed one on the other, as they would have been had they been contained in a pyriform sac, but set at equal short distances apart, as if kept in their places by the membrane of the disk that enveloped them.

Localities.—LOWER OLD RED SANDSTONE, Balruddery, Perthshire; and Leysmill near Arbroath, Reswallie, Tealing, Carmylie, and other places in Forfarshire. The specimens are chiefly in the collections of Lord Kinnaird, Mr. Powrie, and of the Watt Institution, Dundee. One or two are in the Museum of Pract. Geology.

PLATE XIV. [PLATE 25] FIGS. 1 TO 13; PLATE IX. [PLATE 20] FIG. 18?; PLATE XII. [PLATE 23] FIGS. 1 TO 5 (AND 6?).

P. LUDENSIS.

P. major, segmentis corporis omnibus transversis, decimo bis quam longo latiore, penultimo subquadrato vix expanso, supra carinâ percurrenti; caudâ ovali breviapiculatâ obtusicarinatâ: superficie toto plicis curvatis simplicibus ornato.

Under this name I would now describe, with but little doubt of its specific distinction, the fragments of a fine species very abundant indeed in the transition beds of Ludlow, shown as they are in the railway cutting near that town. All the specimens are in the cabinets of Mr. Lightbody and his son. The same species is found at Trimpley near Kidderminster, and we are indebted to Mr. G. E. Roberts for the means of illustrating some points not clear in the specimens at Ludlow.

The materials consist of several body rings of large size, Plate XIV. [Plate 25] figs. 2, 3, 4, 11; a fragment of the caudal joint,

fig. 12; the epistoma; a specimen, fig. 1, showing nearly all the body joints and telson in position, but a good deal obliterated; the serrate bases of the swimming feet, figs. 8, 9; mandibles with palpi, figs. 5, 6, 7; antennæ, fig. 10; and to these must be added certain figures in Plate XII. [Plate 23], showing the antennæ, figs. 1, 2; the post-oral plate, fig. 3; the bilobed (abdominal?) appendages, figs. 4, 5; and possibly the portion of the swimming foot, fig. 6; together with the imperfect caudal joint in Plate IX. [Plate 20] fig. 18. The two last may, however, belong to *P. gigas*, a species very nearly allied, and to which for some time I believed the whole of the specimens referable. Again, there is so much resemblance in certain points to the Scotch species, *P. anglicus*, that it requires nice discrimination to separate the three forms. The characters of the antennæ, and also of the caudal joint, will, I think, be sufficient. And if subsequent observation should tend to show that this "Tile-stone" species is the opposite sex of the *P. gigas*, it will still have been worth while provisionally to separate them.

Body Joints.—The complete specimen, Plate XIV. [Plate 25] fig. 1, shows that the body was not greatly elongated, the segments being all rather widely transverse, the seventh, for instance, being fully four and a half times as wide as long; the eighth and ninth are gradually narrower, but the tenth still shows a width two and a half times greater than the length, while in *P. anglicus* the corresponding joint appears to have been no more than one and a half times the length (see Plate V. [Plate 16] fig. 1).

The penultimate joint is squareish, or rather inversely conical, not much expanded below. It is about one-fourth wider than long (as in *P. anglicus*), and this at the hinder part only. A strong central keel runs down its whole length, covered with large squamæ, and the margins are similarly ornamented.

If the caudal joint, Plate IX. [Plate 20] fig. 18, be of this species, it has lost the terminal apiculus. It is nearly elliptical, the base truncated. It is fully four inches long.

The sculpture of the body rings consists of open semicircular squamæ, flattened along the anterior border and more convex behind, occupying the anterior half of the segment in the front rings, and more in the hinder ones, till, in the eighth and ninth, they nearly cover the segment. On the sides they are more elongate, and, as in other species (*P. gigas*, for instance, Plate VIII. [Plate 19] fig. 5), those on the upper side are more elongate and pointed than those on the lower. All the plicæ are prominent and sharp-edged. There are very few intermediate ones, Plate XIV. [Plate 25] figs. 2,

11, but the surface of the cuticle is generally roughened between the plicæ. Some segments show the plicæ very large, fig. 2, and must have been at least fourteen inches broad. Other specimens in the Ludlow Museum show four or five rings overlapping, and some are subcylindrical, and with sharp edges. The caudal joint (twelfth) is broad-oval and shortly apiculate, less abruptly so than in *P. anglicus*, which, too, has a less regularly oval form, the greatest breadth being below the middle. It is marked all the way down dorsally by a strong carina covered with broad squamæ, and the edges are also squamate, in two or three rows. In the specimen from Trimpley, fig. 12, the sides are marked by oblique radiating interrupted lines.

Epistoma and Labrum (not figured).—This plate is as large as that of *P. anglicus*, Plate III. [Plate 14], and nearly like in all its parts to it.

Antennæ, Plate XII. [Plate 23] figs. 1, 2; Plate XIV. [Plate 25] fig. 10.—These resemble in general form those of *P. anglicus*, but have a more slender shaft, tapering more quickly, and narrower and more conical teeth. The teeth are intermediate in form between the species above mentioned, and *P. problematicus*, the central one being long-lanceolate, and the secondaries narrow, conical, and with coarse striæ. The base of the fixed claw, Plate XIV. [Plate 25] fig. 10, is furnished with a set of stiff spines, as in *P. problematicus*, but the whole chela is proportionably much shorter.

Endognaths, Plate XIV. [Plate 25] figs. 5, 6, 7.—Of these there seem to be two pairs, as in *P. anglicus*, and of very similar shape. The one pair (fig. 5) resembles in all respects Plate VII. [Plate 18] fig. 5, except that it has the teeth more bent down. The joints of the palpus, like those of *P. gigas*, have a squamose ridge along each side, and the ends of the joints are bilobed. The second joint is three and a quarter times as long as broad. This is nearly the proportion in *P. anglicus*, where it is three times the breadth.

The other pair of jaws (fig. 7) have their anterior margin more curved, and the teeth set on a more convex edge than in *P. anglicus*. The first tooth *a* is set more backward, thick, and curved at its base, and all are more curved than in the Scotch species.

The Post-oral Plate (Plate XII. [Plate 23] fig. 3) may belong either to this or to *P. gigas*.

Base of Swimming Foot, Plate XIV. [Plate 25] figs. 8, 9.—These portions are very characteristic in all the species. In this the shape most nearly resembles that of *P. gigas*, Plate IX. [Plate 20] fig. 8, and the teeth are short and blunt, as in that species, but the

neck is shorter. From *P. anglicus*, the shorter form, the short neck, blunt teeth, and convex upper lobe (*a*) overhanging the teeth, distinguish it; but the sculpture raised into thick, prominent, boss-like plicæ is almost identical. The lower edge is tuberculate, and even spinous; our figure does not show this part. A little comparison of this specimen with Plate VII. [Plate 18] fig. 2, will show that both in the upper or front edge (*a*), and on the lower or hinder edge (*b*), the terminal lobe is more prominent in *P. ludensis*. We do not know the other joints, unless Plate XII. [Plate 23] fig. 6, be the penultimate one. It has exactly the form of that of *P. gigas*.

Thoracic? Appendages? Plate XII. [Plate 23] figs. 4, 5.—The nature of these is not understood, nor do these specimens show the characteristic irregular base. But they differ specifically both from the similar appendages in *P. problematicus*, Plate XII. [Plate 23] fig. 16, and from the more perfect one figured in Plate XIII. [Plate 24] fig. 16, by their deep terminal notch. The outer edges are thickened, and the substance of the whole appendage is thick. The lateral plicæ run down in oblique rows on the inner (?) surface, becoming more and more linear, till they become straight lines like the pennæ of a feather; and on the outer side, impressed distant converging striæ cut up, as it were, the whole surface into narrow bands, the terminations of these bands being serrated projections in *P. problematicus*, but in this species they come to an even edge on the notched border.

Ovisacs (?), Plate XIV. [Plate 25] figs. 13, 13*. — The egg-packets (*Parka*), found in plenty with this species at Trimpley, show the membranous veil in several cases. The ova are of considerable size, generally oval, and placed a little apart in the younger packets, fig. 13, but they become hexagonal or polygonal, from mutual pressure, in the older ones, figs. 13*.

Localities.—Base of the OLD RED SANDSTONE, at Ludlow Railway Station (abundant); at Trimpley, north of Bewdley, associated with *Pteraspis Banksii.* (Mr. G. E. Roberts' Cabinet.)

PLATES VIII. AND IX. [PLATES 19, 20].

PTERYGOTUS GIGAS.

SPEC. CHAR. *P. maximus*, 6–7 *pedalis* (?), *capite haud truncato, semiovato; oculis anticis rotundis; segmentis corporis ut in P. anglico,—penultimo expanso emarginato, insuper plano, subtûs carinâ medianâ posticâ: caudâ magnâ ovali, cristâ elevatâ centrali* (*apice emarginato?*).

SYNONYM. *P. problematicus*, BANKS, Quart. Journ. Geol. Soc. vol. xii. pp. 93, &c.

For some years a large *Pterygotus* has been known in the beds of Downton Sandstone (Uppermost Ludlow Rock), worked for building purposes at Kington, Herefordshire, and a description of many of its parts was given by Mr. R. Banks, of Ridgbourne, in the Quarterly Journal of the Geological Society for 1856. Since his description was written, he has continued to labour assiduously to collect the fragments, and has been fortunate enough to discover nearly all the parts of this fine species. He has generously placed these fragile specimens in our hands, and presented a series of excellent drawings, which were formerly exhibited at the Geological Society.[1] In the paper quoted above, the fragments were all considered to belong to the *P. problematicus* of Agassiz, a species for which there is unfortunately very scanty material, but which, as originally described (see below, Plate XII. [Plate 23]) is a Ludlow Rock species identical with one of the Kington fossils, but not apparently with the principal and largest of them, here described, and which in many respects is very like *P. anglicus*.

P. gigas has, in common with the latter species, the open scale-like sculpture on the body rings, and the thick tubercular scales on their margin; the shape of the epistome and head is very similar, but the latter is rounded and not truncate in front. The penultimate body ring is wider and has a short keel on the upper surface only (while *P. anglicus* has one on both sides above and below), and the tail joint or telson appears to be emarginate instead of pointed. But if this character should be deceptive, there can be no doubt of the specific difference, since this joint is furnished with a most remarkable elevated crest or ridge nearly half an inch high, which is quite absent in the Scotch species.

[1] See Quart. Journ. as above, note to p. 97. It ought to have been named after him, had not a much smaller Kington species been already distinguished by his name.

As the fragments indicate a species of the largest size, the above specific name will not be inappropriate. The size of the chelate antennæ exceeds that of any known species.

There are two species in the Kington beds, *P. gigas* and *P. problematicus*, and it was of course possible that some of the parts assigned to the former might belong to the latter species. The subsequent discovery of nearly all the parts of *P. problematicus* shows that in this instance the fragments have been rightly collocated.

Head or Carapace, Plate VIII. [Plate 19] fig. 1.—Nearly semioval, convex, the width three inches and three quarters at the broad base, probably greater than the length. The specimen being imperfect behind, the true length is not known, but the portion preserved is three inches and a quarter long. The eyes are very large, three quarters of an inch long, oval and prominent beyond the margin. They are placed very near the anterior end, and the space between them on the margin is about an inch and three quarters, while between the convex inner edges of the eyes it is about an inch and a half. The anterior border is arched and very slightly angular in front, with a crenulate edge. The sides are convex (their margin not visible).

In the centre of the carapace, and forming an equilateral triangle with the eyes, is an elongate tubercle. The general surface appears somewhat rugose.

Epistoma, fig. 2.—The proportions of this plate and its sculpture are very like those of *P. anglicus;* and the specimen figured indicates this part to be quite as large as that in Plate III. [Plate 14] fig. 7. The plicæ on the upper or front portion (*a*) are crowded, and but slightly curved ; those further back are semicircular or even semioval, while those near the apex of the side lobes are narrower and pointed as in the cognate species. Similar but smaller plicæ occur down the centre lobe, which does not appear to have prominent elongate scales, nor is it convex as it is in *P. anglicus*. Its base *c* is broad and spear-shaped.

Body Rings.—The anterior body rings, fig. 3, bear the squamæ only on their front half, and these are less curved and less crowded than in the corresponding segments of *P. anglicus*. The edge of the plicæ is thickened. Figs. 4 and 5 must represent large segments from a portion of the body further back than fig. 3, for the squamæ cover the whole lower surface of the segment (fig. 5), and the greater part of the upper side (fig. 4). They are greatly more convex than in the Scotch species, the posterior ones especially being parabolic or even pointed in form, frequently three-tenths of an inch long and

broad. Fig. 5 shows the closely squamate lateral edges of the segment, which are convex and rounded in the forward portion and sharply keeled behind. The front margin in both of these segments is contracted, for articulation with the previous joint, and has a broad groove running along its whole length. The hinder angles are a little produced.

Penultimate segment, figs. 6, 7, 8, 9, and Plate IX. [Plate 20] fig. 15.—This joint is much wider than long, in the proportion of four inches and a half to two inches and a half; some specimens must have been fully five inches long, and therefore nine or ten broad. The segment is widest and flattest at the hinder end, the margins are compressed and keeled, except at the thickened and contracted base, and the angles (fig. 9) pointed and produced. The upper surface (fig. 7) is gently convex, but without any ridge, while the lower (?) fig. 6 has a short thick keel extending half way up. It terminates on the hinder margin of the segment, which is rather deeply notched at this point. The surface is thickly covered with plicæ, both above and below, but they are much more prominent on the lower (keeled) surface than on the other, where they are mere surface markings and often obliterated. They cover the whole of the segment, but are less thickly placed towards the hinder margin, at least on the under side (fig. 6). The margin itself is tubercular.

The squamate keeled lateral borders are ornamented with several (about four or five) rows of oblique thick plicæ, more prominent and larger on the lower side; these are continued from about the anterior fourth of the segment, where the keel commences, to the pointed hinder angle. Similar, but still larger, plicæ cover the central keel, Plate IX. [Plate 20] fig. 15*a*, and numerous shallow folds run obliquely backwards from the sides to the keel.

Telson or Tail-Joint, Plate IX. [Plate 20] figs. 16, 17. — The dimensions of this joint give the best indication of the size to which the species grew; its length was full five inches and the width four and a half. The largest specimens of this part in *P. anglicus*, Plate V. [Plate 16] fig. 5, are rather longer but narrower. The general shape was that of a broad and pretty regular oval, but truncated at the base, and emarginate at the apex.[1] The under side, fig. 15 *b*, is flat, except at the origin of the joint, while it is somewhat convex; the median line is even concave. Oblique folds or lines, like those on the penultimate segment, occur on the forward half. The upper side is also flattened, but furnished along its whole length

[1] Plate IX. [Plate 20] fig. 15, is the only specimen which shows the apex. Perhaps there *may* have been a short central apiculus, as in *P. anglicus*.

with a great central keel, rather thick at its origin, but becoming narrower and more elevated (six-tenths of an inch high in the centre), and then decreasing towards the tip.

Sculpture as in the preceding segment. The blunt ridge of the central keel is covered with small squamate plates, and the margins have four or five rows of oblique elongate ones. The general surface is bare of plicæ, except near the base, where they are numerous and prominent both on the upper and under sides.

Appendages.

Chelate Antennæ, Plate IX. [Plate 20] figs. 1, 3. — Fragments only are yet found; the large base of the fixed claw, fig. 1, is about five inches long to the first tooth (in the largest *P. anglicus* it is not more than three inches and a quarter), and one inch ten lines broad (nearly of equal breadth throughout). The articulating edge (*a*) is long and oblique, the joint narrowing considerably into the serrate claw. Of this portion (*b*) there is but little preserved, but it shows the chela to have had broad (probably subovate) cutting teeth, as well as numerous close set smaller ones. These last are short-conical near the base of the fixed claw, and coarsely striated parallel to their sides, the striæ branching from above downwards. Further out (as shown in the separate specimen, fig. 2, which may be the free claw) the smaller teeth are lanceolate and narrow, and the striæ parallel. These striæ are very closely set, much more so than in any other species. These teeth appear to have been irregular in size, and much crowded; a third specimen (fig. 3) shows three kinds,—the small lanceolate one *a*, larger subovate secondary ones *b*, and one a great striate tooth *c*,[1] apparently the median one (see Plate VI. [Plate 17] fig. 5), which is coarsely ribbed, and is besides serrate on the inner edge.

The *endognath* has somewhat broader and shorter teeth than that figured in Plate VII. [Plate 18]; and the second maxillary piece is more curved anteriorly. Mr. Banks' cabinet contains both.

Of the palpi (Plate IX. [Plate 20] figs. 5–7) only fragments are left. Fig. 5 shows four joints connected, but all compressed in a direction perpendicular to their length. Their diameter is half an inch, and their proportions may be compared with those shown in Plate VII. [Plate 18] fig. 4. The second joint *d* is rather longer, and the third *e* not quite so long as in *P. anglicus*. The other figured

[1] A similar tooth (?) has been figured in *P. problematicus*. See Quart. Geol. Journal, vol. viii. pl. 21, fig. 2 *b*.

fragments are less distorted; fig. 6 shows the fourth joint fully one inch and a half long, with the tip expanded and bilobed. In fig. 7, one of the lobes bears a fringe of spines. All the joints show elongate squamæ on their outer side.

Swimming Foot, Plate IX. [Plate 20] figs. 4–9.—The great basal joint, fig. 8, with its serrated tip, closely resembles in form and sculpture that figured in Plate VII. [Plate 18], the chief difference being the greater width of the foliaceous base, and the more backward position of the notch at the point of attachment for the succeeding joints. The serrate terminal lobe, figs. 4 and 9, has broad stout teeth, as usual, thirteen in number, slightly curved, the uppermost broader and shorter than the rest, the lowest *b* a rounded lobe as broad as the two preceding teeth taken together. The teeth are shorter than in *P. anglicus*, especially the upper ones, so that the outline of the serrate edge is more curved. The perfect specimen is only three inches and a half long by two and three-quarters broad, but fragments indicate a size equal to the largest specimens of the Scotch species.

Of the other joints of the swimming foot only two or three specimens (figs. 10–12) have occurred. Fig. 10 shows the upper surface of the right-hand swimming foot, with two complete joints; the fourth (*m*) and fifth (*ca*), with a portion of the great penultimate joint *p**. The latter joint is better shown in another fragment, fig. 10, which is in close juxtaposition, and has a fragment of the fifth joint *ca* attached to it.

The fourth and fifth joints closely resemble those of *P. anglicus* (see Plate VI. [Plate 17]), but the form of the penultimate or propodite is as usual characteristic. It is oblong, two inches and a half in length by one and a half broad, and is but little broader at one end than the other. The upper or proximal end is deeply bilobed, as in *P. punctatus*, the lobes being apparently equally prominent, and the distal or outer end is trilobed; this is partly seen in fig. 10, but much better in fig. 11, where the outer lobe *a* is pointed and prominent, the middle one rounded and shallow, and the inner *c* truncate: the last forms nearly a straight line ending in a sharp angle against the straight inner margin.

Both outer and inner margins of the penultimate joint are serrate with elongate appressed squamæ, and the surface of the preceding joints (the fourth especially) has close and rather elongate plicæ.

Of the terminal palette we have no trace; its probable shape is given in the dotted outline.

Only the *metastoma*, fig. 13, remains to be described. It is greatly

like that of *P. anglicus*, Plate VI. [Plate 17], and chiefly differs in the more contracted base, and large open plicæ of the surface. The notch is somewhat deeper. It may have been smooth over the hinder portion, as in Plate XII. [Plate 23] fig. 3, which is the same or a closely allied species, and may be noticed here, though possibly it belongs to *P. ludensis*, above described.

Plate XII. [Plate 23] fig. 3.—This post-oral plate, in its anterior portion, a good deal resembles that figured in Plate IX. [Plate 20], the notch being a little less deep only. The shape is much more elongate than in *P. anglicus*, the length being as seven to four; the width is greatest at the anterior third, and the general shape ovate. The plicæ are large and open, and are confined to the anterior portion about the notch.

The basal joint of the swimming foot (fig. 6), found at the same locality, is in almost every respect like that of *P. gigas*, having the teeth broad and short.

Locality.—Downton Sandstone (UPPERMOST LUDLOW ROCK) of Kington, Herefordshire. (Cabinet of Mr. R. Banks, of that place.) Some specimens, presented by that gentleman, are in the Museum of Practical Geology. Plate XII. [Plate 23] figs. 3, 6, are also specimens in the Museum, collected by Mr. A. Marston, of Ludlow. They were found at the Ludlow Railway Bridge, in the passage beds at the base of the Old Red Sandstone.

PLATE XII. [PLATE 23] FIGS. 7–16, 20, 21; AND PLATE XIV. [PLATE 25] FIGS. 16–18.

P. PROBLEMATICUS.

P. magnus, segmentis corporis ornatissimis,—plicis minutis creberrimis inter majores mixtis (segmento ultimo transverso, nec expanso, subtûs carinâ brevi medianâ ?): antennis dentibus longis, rectis, remotis.

SYNONYM. *P. problematicus*, AGASS., in Sil. Syst. (1839), p. 606, pl. 4, figs. 4, 5 (*? Sphagodus pristodontus*, AG., tooth only, ib. fig. 6). STRICKLAND and SALTER, Quart. Journ. Geol. Soc., vol. viii. pl. 21, figs. 1, 2; Siluria, 2nd ed. pl. 19, figs. 4–6.

As this is the principal, if not the only species in the true Upper Ludlow Rock, which has the usual semicircular ornamental plicæ, it is to this that the name *problematicus* should be given, and, fortunately, on one of the minute original fragments figured in the "Silurian System," the small intermediate plicæ are to be seen marking the species more definitely.

The large chela, figured as above under this name, by the late Mr. Strickland and myself, proves to be really an appendage of this same species, at least it is always associated with it in the same bed. Again, the antennary portions, fragments of body rings, bases of the swimming feet, post-oral plate, &c., figured on Plate XII. [Plate 23], are all found in the Whitcliffe, Ludlow, or other localities of the Upper Ludlow Rock, and clearly differ from the corresponding parts in *P. punctatus*, the only other large species occurring with them, as well as from those just described, which are characteristic of the beds of passage above the top of the Ludlow series. *P. problematicus* may now, therefore, be considered an established species, and the cabinets of our Ludlow friends, Messrs. Cocking and Marston, have furnished many of the materials. It occurs, too, in plenty, as Mr. Lightbody's researches show, in the transition beds beneath the Old Red Sandstone, Plate XIV. [Plate 25]; and Mr. J. Harley, to whom we are indebted for much valuable help, has been fortunate enough to detect its fragments far up in the cornstones of the Old Red itself, a higher limit than the genus had been known before to attain.

[If the large fragments from the transition beds above quoted, and figured on Plate XIV. [Plate 25], be of the same species, as the sculpture indicates, the body segments attained a very large size, nearly three inches from back to front. As it is possible these may belong to a different species, I will describe these portions first.

Carapace (?), Plate XIV. [Plate 25] fig. 16.—A fragment, three inches by two and a half, has the surface sculptured, unlike the body rings, *i.e.*, much more finely marked, and without the regular increase in size and curve of the plicæ backwards. The anterior ones are nearly as much bent as the hinder ones though smaller—all are but slightly prominent, and are covered by numerous smaller plicæ.

Body Rings, Plate XIV. [Plate 25] fig. 17.—One of the broad abdominal rings, two inches and three-quarters from back to front: the articulating front margin is rather deeply concave, and its edge is obscurely striate longitudinally (like fig. 3). The plicæ are very numerous and close-set, not so large as in *P. anglicus*, or so straight on the forward edge, where, however, they are very closely packed. They are more open posteriorly, and cover more than half the segment, interspersed with very numerous minute semicircular plaits.

Another piece (fig. 14) is here considered as belonging to this species, but it only shows the interspersed plicæ over part of the

surface: and it quite possibly belongs to *P. ludensis*, or even to a new species.

Penultimate Joint, Plate XIV. [Plate 25] fig. 18.—Of this we have only the lower surface; and as the plicæ are restricted to the upper portions, and only a few small ones are interspersed, it is possibly not *P. problematicus*, but of the same species as fig. 15, mentioned above. The width is greater than that of the same joint in *P. anglicus* or *P. ludensis*, being three inches and a half, while the length is only two and a quarter, (or as fourteen to nine,) which is about the proportion in *P. gigas*. The joint is not expanded posteriorly as in that species, and the plicæ are semicircular, not pointed, on the lower side.]

In the true Ludlow Rock but few body joints have been met with, the two best are figured from Mr. J. Harley's collection, viz., Plate XII. [Plate 23] fig. 20, must be one of the thoracic rings, and fig. 21, probably the tenth or last but two of the segments. Both show the minute interspersed plicæ very clearly, and these small plicæ extend over nearly all the segment, while the larger ones are confined to the anterior half.

Telson, as yet unknown, as also is the *epistomian plate*.

Antennæ, Plate XII. [Plate 23] figs. 7–10. — Fig. 10 is most probably part of the stem, and shows the large and small plicæ in perfection. Figs. 7 to 9, the large characteristic chelæ, which can scarcely be confounded with any other species, the teeth being so much elongated. Fig. 7 is the fixed claw, with a widely expanded and largely dentate base.[1] The shaft is parallel-sided (not tapering as in *P. ludensis*), and the teeth long-lanceolate, the large one being much longer than the diameter of the shaft, (in fig. 7, fully three-quarters of an inch long,) the secondaries three or four on each side of it, with small teeth interspersed, all linear-lanceolate, erect and remote, not crowded at their bases. In the fixed ramus they are either erect or (fig. 8) point forward a very little.

The striæ on the teeth are very fine and close,[2] oblique some-

[1] See *P. ludensis* (Plate XIV. [Plate 25] fig. 10), for a similar chela.

[2] See also Strickland's figure, quoted above. There is one lanceolate fragment (2 *b*) in that figure, here reproduced, fig. 9*, which is striated finely like the teeth. It is serrated all down one side. Its nature is quite doubtful; but it is associated with the antenna; and as the large primary tooth in *P. gigas* (Plate IX. [Plate 20] fig. 3) is serrated posteriorly, it is possible this may be the case in one of the chelæ of the present species. There is a small conical uncinate appendage in the same figure, Geol. Journ., that is yet unexplained.—Quart. Journ. Geol. Soc., l. c.

what on the great tooth, and more direct in the smaller ones. In *P. gigas* and *P. ludensis* they are coarser, and the teeth broad. The great terminal mucro is as broad and long as the primary tooth, or even longer, and is bent at right angles to the shaft.

Swimming Feet, Basal Joint, Plate XII. [Plate 23] figs. 11–14.—Several fragments have been found of the great basal joint, and one tolerably perfect from the Whitcliffe, Ludlow, fig. 11. It shows a wide-expanded basal lobe, and the whole extent of the serrate tip, with the usual number of teeth (thirteen, or rather twelve in this specimen); and in fig. 14, the upper tooth being obsolete. Fig. 13 *a*, from Ludlow, shows the full number.

The lobe in front of the teeth is arched and thickened in all the specimens, (a character in which this species differs widely from

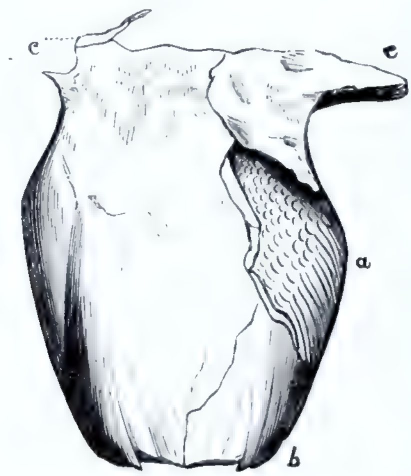


FIG. 12.

Pterygotus problematicus, Ag., thoracic or abdominal appendage ? nat. size. Comus Wood, Ludlow, in Upper Ludlow Rock (Cabinet of Mr. J. Harley, King's Coll.)

P. anglicus,) and the second tooth is more than twice the breadth of any of the others, conical, and but little curved; the remaining teeth are long, straight, narrow, and separated by about their width from each other in large specimens. These elongate teeth are very distinctive of the species. I believe I am not mistaken in referring Agassiz's figure of the *Sphagodus* tooth to this portion.

Metastoma (Plate XII. [Plate 23] fig. 15, Plate XIV. [Plate 25] fig. 19, is cordate-ovate, narrower at the bilobed end, and has its greatest width below the middle (our figure does not express this well), becoming angulated at that point. The notch is deep, the lobes rounded (the base is broken off, surface marked with open

squamæ, but only near the upper end and about the notch. This post-oral plate is the broadest of any species known.

Fig. 16 is a plate of the same nature as those found with *P. ludensis*, and is possibly a thoracic or abdominal appendage, though, as no species are known with any such attached, its nature is quite doubtful. The small crenate fragment, fig. 17, probably belongs to it; a similar piece is attached at *c* to fig. 16. [The entire form is better seen in *P. arcuatus*, Plate XIII. [Plate 24] fig. 16, viz., a lobed broad emarginate plate (*d*), in the wide notch of which is attached the truncated sub-oval plate *a*, *b*.] A more perfect specimen is here added in a woodcut, showing the thickness of the plate on the one side of it. The obscure converging lines ending in serrations on the border are exhibited on one surface; on the opposite, the oblique close plicæ running into parallel lines towards the margin, very like the segments of a feather.

The base *a a* is much extended on each side, and in this respect seems to be different from the figure above quoted, Plate XIII. [Plate 24], which probably belongs to *P. arcuatus*.

Localities.—UPPER LUDLOW ROCK, Whitcliffe, and many places near Ludlow (Ludlow Museum and Museum of Pract. Geology; Cabinets of Messrs. Lightbody, Cocking, J. Harley, and A. Marston). Kendal, Westmoreland (Museum of Pract. Geology). Ludlow Bone Bed, Ludlow; Downton Sandstone of Bradnor Hill, Kington. (Mr. R. Banks' Cabinet.) BASE OF OLD RED SANDSTONE, Ludlow Railway Station (Museum of Pract. Geology). Cornstones of Hopton Gate (Cabinet of Mr. J. Harley).

One of the most widely spread species; it is probably this which occurs in the Upper Llandovery Rock or "May Hill Sandstone" of the Obelisk, Eastnor Park. A woodcut of it is subjoined.

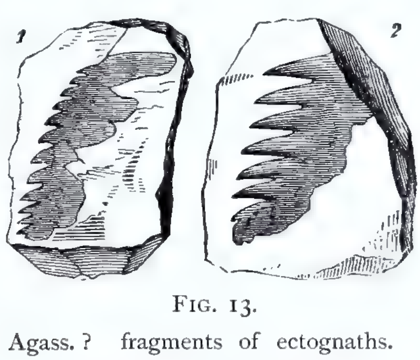


FIG. 13.

Pterygotus problematicus, Agass.? fragments of ectognaths. Eastnor Park, Malvern. (Cabinet of Sir W. Jardine.)

PLATE XIII. [PLATE 24] FIGS. 8, 12, 13, 15, AND 16.

PTERYGOTUS ARCUATUS.

SPEC. CHAR. *P. major, segmentis arcuatis, plicis semicircularibus parvis, nec squamulis minutioribus intermixtis.*

The name is applied to a large and fine species, of which several fragments occur in the Lower Ludlow Rock of Leintwardine, along with the more common *P. punctatus*, Plates X., XI. [Plates 21, 22]. It is clearly distinct from that species, but except for the total absence of any minute interspersed plicæ, the body segments might be easily mistaken for those of *P. problematicus*, to which it is closely allied; and with it, in the same beds of Lower Ludlow Rock, occur *antennæ* (fig. 8), the obscure appendages (fig. 16), swimming feet, maxillæ, and other oral apparatus, differing specifically from those of *P. problematicus*, and yet more distinctly separated from the portions of *P. punctatus*, found in the same beds. Of these fragments the body segment must receive the name, the other pieces being only provisionally arranged with it. They all resemble the corresponding parts in the Upper Ludlow species.

Body Segments.—Fig. 12 is clearly, from its shape, the second body segment, seven inches broad and more than one inch and a half deep. It is curved, and more oblique laterally than in *P. anglicus*, the sides forming an angle of 65° with the base. The anterior edge is much more sinuated than the posterior, owing to the deep excavation to receive the first segment; but the central part is strongly arched forward on both margins. The lateral anterior process *a* is broken off, but enough remains to show it was prominent. The sides are oblique, inclined forward at an angle of 80° from the posterior angle, which is rounded off. The margin is crenulated, the prominent minute sculpture confined to the anterior third, but continued more faintly over a large part of the segment. (The sculpture in the thoracic segments of *P. punctatus*, Plate X. [Plate 21], though not carried over a much larger part of the surface, is far more prominent and remote.)

A specimen, crushed longitudinally (fig. 13), shows that the species was rotund in section, as in *P. punctatus* and others.

Antennæ.—In all probability Plate XIII. [Plate 24] fig. 8, represents the antenna of this species. Its resemblance to those of *P. problematicus* is very close. The shaft is linear, the long end

turned abruptly up, and the teeth straight, narrow, and remote, as in that species ; but the chela is much more slender, three inches and a half to four inches long, and the larger central tooth is scarcely longer than the diameter of the shaft itself; while the secondary teeth, some of them at least, approach it more nearly in size. The tooth at the base of the large terminal mucro is appressed against it, and the mucro itself (Plate XI. [Plate 22] fig. 3) is sometimes oblique. All the teeth are finely striate, the striæ tending obliquely backward on the principal teeth. There are numerous sharp, conical, minute teeth between the secondaries.

Endognaths (*Maxillæ?*)—Most probably Plate XIII. [Plate 24] fig. 15, represents the first or second pair of these organs, and it is pretty clearly referable to *P. arcuatus*, and not to *P. punctatus*, which has much shorter and blunter mandibles. (Plate XI [Plate 22] fig. 6.) It is elongate, or even falcate, the upper lobe *a* greatly convex, the posterior portion (*f*) drawn out laterally instead of backwards ; the surface closely sculptured all over. The teeth are not oblique, straight, and conical as in *P. punctatus*, but lanceolate and curved, and directed outwards. About ten or eleven are free, the rest confused, either in a horny plate or mixed with setæ. In this particular, and in the production of the lower lobe *b*, it resembles *P. punctatus*, but the great curvature and elongation of the plate distinguish it.

Base of Swimming Foot, Plate XI. [Plate 22] fig. 10. — Most probably, from the very convex form of the anterior edge, and the greatly elongate teeth, this belongs rather to the present than to *P. punctatus*. [Plate XIII. [Plate 24] fig. 14, may, perhaps, represent this part in the latter species.]

Post-oral Plate, Plate XV. [Plate 26] fig. 5.—Found at Leintwardine, by Mr. Alfred Marston. It differs from the corresponding plate in all the species, having the lobes of the apex narrow, and nearly their own width apart, the sinus between them being very wide and shallow, instead of a simple deep notch. The plate is cordato-lanceolate, for the upper two-thirds it is oval, the greatest width being rather below the upper third ; the base is rather suddenly contracted, and tongue-shaped.

Thoracic (?) *Appendage*, Plate XIII. [Plate 24] fig. 16. — This has been already alluded to (p. 253), as probably belonging to the species. It is more perfect than any other specimen, though only the impression of one side. The large ovate terminal plate *a b*, shows well the gradation between the ordinary plicæ and the long lateral plaits, the middle line is bare of any ornament. At the apex are seen two or three of those impressed lines, which are so much more

conspicuous on the opposite surface, and which seem to divide the plate into laciniæ, *a*. The plate is indented at its basal end, corresponding to the central depression (ridge in the cast) of the preceding joint. This joint is very irregular in shape, the lobes on one side, *d*, being single, on the opposed side *c* double. Both are marked with minute plicæ near the edges.

Locality.—The above-mentioned fragments have all successively come to light during the active researches of the Ludlow geologists in the quarries of LOWER LUDLOW ROCK at Leintwardine, particularly in one at Church Hill. There are many new Crustacea to be described from the same quarry, of one of which the head portion has been accidentally introduced into this plate. Plate XIII. [Plate 24] fig. 17. See also p. 190, *suprà*.

PLATES X. [PLATE 21], XI. [PLATE 22], AND PART OF XIII. [PLATE 24].

PTERYGOTUS PUNCTATUS.

P. magnus, (5–6 *pedalis?*) *capite*——(*?*), *segmentis omnibus squamulis remotis prominulis ornatis,—in articulis posticis per totum annulum sparsis; chelis antennarum elongatis: palpis longi-fimbriatis. Pedibus natatoriis articulo terminali elongato, penultimo expanso.*

Of this very large and distinct species various fragments have from time to time come to light, and have been communicated by our friends, Messrs. Lightbody, Cocking, and Marston, of Ludlow, and especially from the cabinet of H. Pardoe, Esq.

They are from the quarry at Leintwardine, Shropshire, in the Lower Ludlow Rock, where many fine starfish and other rarities have been newly discovered. (Siluria, 2nd edition, p. 140.)

There is evidence of at least three, if not more, of the thoracic rings. The hinder segments were decidedly longer in proportion to their width than in the *P. anglicus* or *P. gigas*. We have also the swimming paddles, which, without the great coxal joints, were seven inches long, expanded in the penultimate joint and attenuated at their tips; of the mandibles, the palpi of which are strongly fringed with long curved processes, and of antennæ, with slender pincers at their terminations, and armed with numerous small conical teeth. As all these parts present distinctive peculiarities from other species, and as the tuberculation on the various specimens found in this bed agrees in character, it is fair to combine them as a single species, and figure them all upon one plate.

Of the carapace or eyes we have yet no trace. But the *epistoma* (fig. 1) presents us with a singularly neat character for the species. The upper portion of this organ is broadly sagittate or spear-shaped, as in other species, and offers a wider basal angle than that of *P. anglicus*, but the outer portion, which is quite straight and linear, (instead of being clavate,) is bilobed at the tip; and from the deep terminal notch a raised central line is continued nearly all the way up the linear portion, and terminating in a slight prominence. The whole piece is smooth.

Of the first *body ring* a fragment an inch and a half long and one inch wide is figured (Plate X. [Plate 21] fig. 2). It is the semi-circular sweep of the outer edge of the segment, where it fits into the scooped out portion of the succeeding (second) one. The rounded margin *a* is serrated, the serrations pointing backward. The sculpture is very minute, prominent, and confined to the forward half, except a few marginal plicæ on the hinder edge. All are longer than wide. Fig. 2*a* shows them magnified. Fig. 3 is without much doubt the second thoracic segment. It is wider at the sides than in the middle, and turns up abruptly at the forward angle to form the characteristic process. Fig. 4 appears to be a larger specimen of the third ring, it has the same characters of ornamentation. In both the central portion is less arched than in *P. anglicus* or *P. arcuatus*, and the sides less oblique and minutely crenulate. A narrow (articular?) furrow runs along the middle portion of the anterior edge, followed by a convex ridge, which is bounded by a row of prominent minute tubercles extending a good way out, and nearly to the lateral margins. Behind this the anterior third of the segment is occupied by the sculpture, which is much more prominent and tubercular, and less scale-like than in the large Scotch species.

The occurrence of this line of tubercles enables us to connect with the species some very curious fragments, one of which is here figured (fig. 8) with one or other of the body rings. When first viewed the piece appears quite anomalous, the extended ends giving the general form much the aspect of the epistoma, but a closer examination shows that it has an upper surface *b*, and the impression of the lower side *c*, each with the sculpture pointing backwards, and with no room for a median lobe. Of the *epistoma* we have now obtained specimens (fig. 1, as above described), and it remains therefore to explain this piece as one of the body rings, obliquely pressed, (probably the exuviated crust only,) the angular edge being indicated at *a*, and one surface (the inferior) *c*, being less disturbed

and altered in shape than the other, *b*. The dotted lines will give a notion of what was probably the complete form. Fig. 9 is probably a similar fragment. Figs. 10 and 11 have as yet no explanation. Fig. 7 shows the true outline of another ring, which has been compressed vertically in the rock, instead of laterally. These specimens of course give the true idea of the convexity, which was very great. The form was almost cylindrical.

Of the intermediate rings we have very few fragments, but several hinder rings, which must have been near to the extremity both from their form and their being quite covered with the elongate tubercular plicæ.

Plate IX. [Plate 20] fig. 7, from the cabinet of Mr. Marston, represents probably the penultimate ring. It is two inches and a quarter long by two inches at its truncated extremity, which is rather wider than its base. The shape is thus nearly square, the

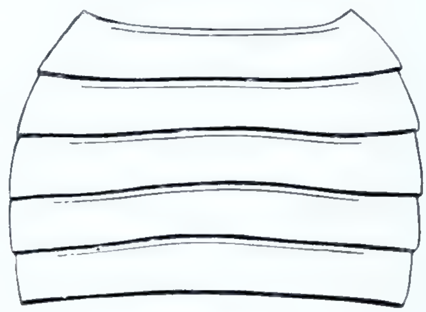


FIG. 14.

Anterior body rings of *Pterygotus punctatus*. The first segment lost. From Lower Ludlow Rock, Leintwardine. In the collection of Mr. J. Harley.

sides are but very slightly (perhaps not at all) curved, nor is the base *a* contracted or the distal end *b* expanded or produced, as in *P. anglicus*. The edge is crenate. Plate XIII. [Plate 24] fig. 5 is from the Upper Ludlow Rock.

The caudal joint (telson) is yet wanting and should be sought for, as in all probability it was not unlike that figured on Plate VIII. [Plate 19], fig. 11 has possibly something to do with it.

Mr. J. Harley, of King's College, has found a small specimen, doubtless of this species (woodcut, fig. 14), since the plate was finished. It has the second to the sixth rings united, and the pyramidal form of the front ring is very marked.

Appendages.

Antennæ.—Of these great pincer-like organs only two chelæ have been found, one three inches and a half long, but these are quite different in proportion from that of *P. anglicus.* The shaft is much longer and slenderer, being quite eight times as long as wide, and not much thicker at the origin than near the tip. The teeth are much shorter, the central one is as long as the diameter of the chela itself, and placed beyond the middle; two other primaries nearly equal in size and a secondary tooth are outside it, while only minute teeth with a single primary near the hinge occur on the proximal half. As many as twenty of these small conical teeth may be counted in the inner half, and eleven or twelve on the outer. The primaries are broad-conical (not ovate), striated and directed backwards, and are not crowded at their bases by the smaller teeth which vary much in size, but are all of them more or less conical in shape like the larger ones. The terminal mucro is lost in both the specimens; a few tubercles occur on the shaft near the end, fig. 2 *a.*

Endognaths and Palpi, figs. 5–8, and Plate XIII. [Plate 24] figs. 9–11.—There are several specimens and they present some strong characters for the species. Plate XIII. [Plate 24] fig. 9, and Plate XI. [Plate 22] figs. 7 and 8, show portions of the palpi, and fig. 5 an endognath with its entire palp attached, and in the proper position in respect of the great swimming foot *c.* From this specimen it would appear that the remarkable spines of the palpus were directed forward. Figs. 8, 9, show the great size these appendages obtained.

The teeth of the maxillary piece (fig. 6 *a a**) are small, short, and obliquely conical, not curved, and as in some other species striate; there are about seven distinct, and six smaller ones, which last are either connected by a horny plate (as in *P. anglicus*), Plate VII. [Plate 18] fig. 5 *b*), or are confused with setæ; the state of preservation does not permit us to decide which. The margin near the teeth is punctate, indicating the presence of hairs or setæ. In some specimens the teeth are narrower and sharper.

[Fig. 10, though found in the same bed, must evidently belong to a distinct species, and has been already referred to *P. arcuatus.* Fig. 11 is probably a second pair of jaws (endognaths), as already indicated in other species.]

Palpi.—The great palpi (of which fig. 6 only shows the base at

S 2

b, and fig. 5 a nearly perfect one *in situ*) are broader at their base than the length of the serrate border *a*. They consist of only five joints, all except the basal one bearing (a pair? of) curved processes, while the terminal one, *g* in fig. 8, might even be considered as an additional joint.[1] The specimen (Plate XIII. [Plate 24] fig. 9), obtained since Plate XI. [Plate 22] was completed, shows all the joints complete, and these resemble Plate XI. [Plate 22] fig. 7, in their elongate form. Fig. 5 has much shorter joints and may very possibly belong to a different pair of maxillæ. In this figure, the first joint is very broad and large, subquadrate, tapering but little, rather longer than broad, and bears apparently no curved process. Its edge is spinose, fig. 6 *b*. The third, fourth, and fifth are, in figs. 5 and 8, not very different in size and nearly square, while in fig. 7 the proportions are longer. All have the great curved spines placed about the middle of the joint.

In the perfect palpus (Plate XIII. [Plate 24] fig. 9) the proportions of the joints are as follows. The basal one is smaller than the second, about two-thirds its length, and of a roughly triangular or trapezoidal shape, the base smallest. The second is longest—half as long again as its breadth; the third and fourth much shorter, the fifth only half as long as broad, and bearing one curved spine at its outer angle, and the other (*g*) at its tip. The second, third, and fourth joints are subcylindrical, convex on their outer margin, and bear the curved spines about the middle of the joint.

The terminal articulation (*g*), if it be a separate joint, consists only of the curved process; but it is probably only the opposite spine of the fifth joint, seen obliquely, and in this view there would be five joints only to the palpus, each joint bearing a pair of processes, as is certainly the case in Plate XIII. [Plate 24] fig. 11.

The processes themselves are directed obliquely outwards and forwards; they are long, curved, sabre-shaped, and much compressed, fully three times as long as the width of the joints, to which they are attached by a swelled base. They are striated longitudinally, the striæ, eleven or twelve in number, sharply impressed, not continuous except near the tip, but interrupted alternately (Plate XIII. [Plate 24] fig. 10) for wide spaces, so that the number of striæ appears little more than half what it really is. Nor are the striæ quite parallel to the sides, for they abut obliquely against the concave

[1] Although the specimens from Church Hill look as if there were only a single process to each joint, yet, as in the palpus of this species, figured in Plate XIII. [Plate 24] fig. 11, there is a pair of these organs, it is most likely all the other specimens had two. In this view the two processes *f*, *g*, would belong to the terminal fifth joint.

side towards the tip of the process. Here and there some striæ are stronger than the rest.

Near the base of the processes the striæ are still more interrupted and run into short impressed lines or puncta.

Plate XIII. [Plate 24] figs. 5, 6, 7, 11, and 18.—These are from the UPPER LUDLOW ROCK. Fig. 11 is a very perfect joint of the palpus, with both spines attached; and figs. 5 and 6 show the characteristic long plicæ; fig. 7, part of a chela probably of this species. Fig. 6 at least would answer best to one of the long joints of the antennæ; it is but a cylindrical fragment of the proximal end, and has the contraction which is visible in the corresponding joint of *P. anglicus*, Plate IV. [Plate 15] fig. 4 *c*. At this part the plicæ are very numerous and small; in the body of the joint they are large, prominent, and elongate, and with the channel-like depression and its bounding ridges, fig. 6*a*, magnified. They are somewhat unequal in size, and set at more than their diameter apart from one another.

Plate XIII. [Plate 24] fig. 18.—There is one other fragment in the Upper Ludlow to which a place cannot be yet assigned, and yet belongs apparently to *P. punctatus*. It is a long strap-shaped piece, two inches and a half long and half an inch broad, and narrowed and rounded at one if not both ends. At *b* it is imperfect. The surface shows the peculiar long tubercular plicæ of the species, at least near the base (*a*) and the opposite end *b*, and the margins are deeply incised by short slits forming nearly square serrations (like those on the edge of the carapace of a crab). This is not exactly the structure of any part of the margin of *Pterygotus*, the usual ornament being that of prominent superficial plicæ or tubercles. The terminal (?) portion *b* differs in not having (so far as the impression shows) this serrate edge, but only a thickened crenate margin and is probably a distinct joint, or may even be accidentally placed where it is. The surface shows elongate plicæ of various sizes, rather thickly scattered.

The *Metastoma* (Plate XI. [Plate 22] fig. 4) is nearly three times as wide as long, widest above the middle, and tapering backwards with straight sides from this point to the blunt posterior extremity; the anterior end is broadest, rounded, and not even emarginate; much less bilobed as in other species. It is thus quite different in shape from that of any other species; its long oval form, blunt ends, and straightened sides enable us to recognise it at once. It occurs three inches and a half long; and in specimens of this size, the width is one inch and a quarter.

The *Swimming Feet* (Plate XI. [Plate 22] figs. 12–15) are very different in proportion to those of *P. anglicus*, the terminal joints occupying a considerably greater length, and being abruptly wider than the rest. Of the great basal joint (*co* in fig. 5) but little is preserved, but a larger specimen, fig. 12, shows it to have been roughly squamose, especially along its basal edge, the narrow squamæ projecting as small spines, the rest of the surface is closely imbricated with smaller plicæ. Pl. XIII. [Plate 24] fig. 14, is very possibly the serrate inner lobe of this joint. The second joint *b* is large in proportion to the rest, and widens from the base to its truncated apex. The third *i* is subtriangular, the blunt apex of the triangle being anterior, and the edge articulating with the next joint nearly straight or but slightly curved. The fourth joint, on the contrary, is an obtuse triangle, of which the broad base is forward and moderately arched, but not projecting as in *P. anglicus*. It contracts rapidly behind, where it has a narrow deep notch to receive the articulating process of the next joint. This, *ca*, is the fifth, a remarkably short wide articulation, almost buried in the concave edge of the great penultimate joint, and curved to follow the convex border of the triangular fourth joint. It is marked by a strong transverse ridge. All these joints may be seen in figs. 5 and 13, but in a far less perfect state than in the fine specimen, fig. 13, presented by my young friend Mr. R. Lightbody, jun., of Ludlow. The penultimate joint *p* is very large, nearly three inches long, and about half as broad. It is oblong, with two rounded unequal lobes, and deeply notched at each end (the distal notch at the end being the deepest), so that the joint overlaps the proximate joints at either end. The hinder margin of the joint is more convex at first, then somewhat excavated, while the anterior margin is straight, or nearly so: the hinder lobes at both ends are larger than the anterior ones, the proximal one, which overlaps the small fifth and fourth joints, being broader and rounder, and the distal one, which abuts against the terminal palette, being long and narrow.

The terminal joint (*d*) is very long, nearly three inches by nine-tenths of an inch wide, elongato-lanceolate, but rounded at the tip, its anterior margin a little convex, and plain-edged half way down, the posterior slightly concave and rather strongly serrate,—the serræ are shallower on the anterior margin, and deepest round the tip.

Locality.—Church Hill, Leintwardine, in LOWER LUDLOW ROCK; Whitcliffe, Ludlow, UPPER LUDLOW ROCK; Kendal, Westmoreland; fragments in UPPER LUDLOW ROCK.

J. W. S.

January 22, 1859.

XIII

ON DASYCEPS BUCKLANDI

(*Labyrinthodon Bucklandi*, Lloyd).

Memoirs of the Geological Survey of the United Kingdom 1859, *pp.* 52—56.

AT the meeting of the British Association in 1849 Dr. Lloyd, to whom science is so much indebted, as the collector and preserver of almost all the known remains of British Labyrinthodonts, gave a description and exhibited a lithographic drawing of a "new species of *Labyrinthodon* from the New Red Sandstone of Warwickshire." An abstract of the description, without the figure, is published in the Reports of the British Association for 1849, p. 56; but it is very brief, the most important points being the indication of "projecting occipital condyles," and the statement that the teeth presented "the usual characters of the genus." The fossil, which is named by Dr. Lloyd *Labyrinthodon Bucklandi*, is said to have been derived from the "Bunter sandstone," but the locality is not given.

In the course of a hasty visit to the Warwick Museum during the past winter (1858), I was struck with the remarkable appearance of this fine fossil, and I saw at once that it was generically distinct from any known Labyrinthodont. Hence, having occasion to refer to it incidentally in a paper which I read before the Geological Society in March last, I proposed a distinct generic name, *Dasyceps*, for it; but I was not at that time aware of the fact that the quarry at Kenilworth, whence the fossil was obtained, is not situated in the Bunter at all, but in rocks of Permian age. The knowledge of this circumstance lent additional interest to the inquiry into the precise characters of *Dasyceps*, which I undertook during a recent repetition of my visit to the excellent Museum at Warwick, where this and so many other important remains are stored up.

The flat cranium, which is 10 inches in length from the middle of

the occipital region to the end of the premaxillæ (Fig. 1, *i*, *w*), has been so split that the upper wall remains attached to the one half of a block of sandstone, while the lower is imbedded in the other; consequently only the smooth inner faces of the cranial bones are for the most part displayed, though a portion of the frontal bones which adheres to the lower half of the cranium exhibits the upper or outer

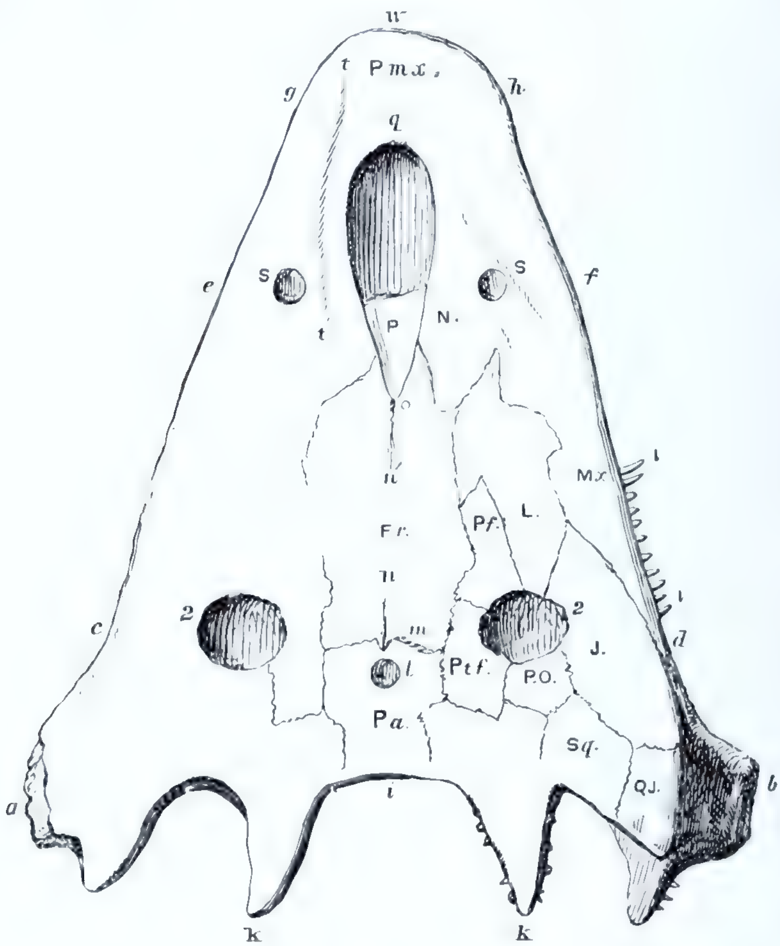


FIG. 1.

surface of those bones, and the character of this surface is well shown by the impressions which remain where the bony plates themselves have disappeared.

The upper half of the cranium is in better condition than the other. It has the form of an isosceles triangle, whose apex is abruptly rounded off, and whose base (the space between the outer edges of the quadrate bones, *a*, *b*, Fig. 1,) measures 9⅓ inches. An inch and a half in front of the posterior margin of the occiput, on the line of the posterior margins of the orbits (*c*, *d*,) the skull measures 7¾ inches in

transverse diameter. Six inches and a quarter in front of the occipital margin, or on the line of the external nares (*e*, *f*,) the transverse diameter of the skull is 5 inches. The postero-lateral angles (*a*, *b*,) of the cranium are truncated, and in front of them the lateral contour sweeps inwards (*b*, *d*,) and is then continued, in a nearly straight line, forwards to the obtuse end of the snout, which measures about $2\frac{1}{2}$ inches in width, half an inch behind its extremity (*g*, *h*). The strong postero-lateral angles of the cranium project for 2 inches behind the posterior margin of the occiput (*i*), which margin is interrupted, between its centre and these produced postero-lateral angles, by two large and stout pointed processes (*k*, *k*,) which project backwards for fully an inch and a half.

In the middle line, $1\frac{1}{2}$ inch in front of the occipital margin, or on a level with the posterior margins of the orbits, the bony substance presents a rounded parietal foramen (*l*) one-third of an inch wide. Just in front of it lies a transverse suture (*m*), separating the parietal from the frontal bones, which is slightly convex forward, and presents in the middle line a slight backward sinuation, whence a median suture (*n*) can be traced for a short distance forwards. At *n'* is what appears to be the anterior continuation of this suture, which terminates abruptly in a broad oval space (*o*, *p*, *q*,) $3\frac{2}{3}$ inches long, and narrow behind, but gradually widening in front, till at $2\frac{1}{2}$ inches from its posterior extremity it attains a width of $1\frac{1}{2}$ inches. The contours of this space are symmetrically and evenly rounded, and where its surface has remained unbroken, as at (*p*), it is perfectly smooth, presenting in this respect a marked contrast to the strongly pitted impressions everywhere left by the adjacent facial bones.

The bony edges which form the boundaries of this area are, in fact, quite sharply defined, and I could nowhere find the least trace of their having been continued into the substance of the matrix which fills the area. I can only imagine, therefore, that, during life, a membranous, or at most cartilaginous, substance must have filled this interspace.

The orbits (2, 2,) rounded spaces about an inch in diameter, are situated very far back, and are remarkably small in proportion to the size of the skull. They are placed about midway between the middle line of the skull and its outer margin. The round external nostrils (*s*, *s*) also proportionally very small, their diameter not exceeding half an inch, are in like manner situated very backwardly, their anterior margins being more than 3 inches from the end of the snout.

On the left side of the fossil (the right side of the skull) there is, between the nostril and the facial fontanelle (as the area *o*, *p*, *q*, may be

termed) a sinuous elevation *t, t,* which is probably the cast of a groove on the outer surface of the face, answering to the anterior of the so-called "mucous-canals" of the ordinary Labyrinthodonts.

Some of the cranial sutures can be traced with tolerable certainty; those in the neighbourhood of the orbits, for instance, between the post-frontal (*Ptf.*), pre-frontal (*Pf.*), post-orbitar (*P.O.*), and jugal (*J.*) bones, are very well marked. The lachrymal (*L.*) appears to enter into the anterior boundary of the orbit, and the maxillary (*Mx.*) extends back to at least the point (*d*), if not further. The frontals (*Fr.*) seem to have been very large bones, extending from just in front of the parietal foramen to the posterior margins of the facial fontanelle, into which they enter. The bone which unites with them at this point I regard as the nasal (*N.*). Its junction with the premaxillary (*Pmx.*) cannot be observed, but I have little doubt that the boundaries of the fontanelle are furnished by three bones on each side, the frontals, nasals, and premaxillaries. The characters of the supra occipital cannot be made out, nor are any sutures distinctly visible in the region between the letters *i, k, Sq.* The latter bone and that marked *Q.J.* are, it is to be understood, only provisionally denominated squamosal and quadratojugale, as I entertain some doubts respecting their homologies.

Dr. Lloyd (supra) speaks of twenty teeth. The specimen is so excessively fragile that some of those which he observed may readily have perished. At any rate I can only find eleven, which occupy a space of 2 inches (*v, v,*) on the left side of the maxilla, and of these only the two anterior ones are in a perfect condition. These teeth are pointed, much curved, and about a quarter of an inch long, their bases having a diameter of three-fortieths of an inch. They are directed outwards, their curved sides being downwards and inwards (in the natural position). They are anchylosed to the margins of the jaw, which exhibits no alveolar groove. Their bases are longitudinally striated, and they present apparently a wide pulp cavity, but I can say nothing respecting their minute structure, as I did not feel justified in detaching any of the few which remain. Obscure traces of teeth are seen in the rest of the alveolar margins.

The inferior half of the cranium (Fig. 2) presents a small adherent patch of the frontals (*Fr.*), and what appear to be the under portions of the bases of the two processes, *k, k.*[1] The matrix at *l* and 2, 2,

[1] I suppose that these are the parts regarded by Dr. Lloyd as the occipital condyles; their nature, however, appears to me to be what I have stated above. I could discover no condyles where I should have expected to find them; but it is possible that they might yet be brought to light by very careful excavation.

presents impressions corresponding with the orbits and parietal foramen, but the most interesting portions of this half of the fossil are the broad bony plates *V*, *V*, separated by a median suture, and the wide, more or less completely circumscribed apertures *x*, *y*, *y*. Of these, *x* appears to be the anterior palatine foramen, whose anterior boundaries are broken away, while *y*, *y*, are the posterior nares. In Fig. 2 I have dotted the outlines of the facial fontanelle (*q*) and of the

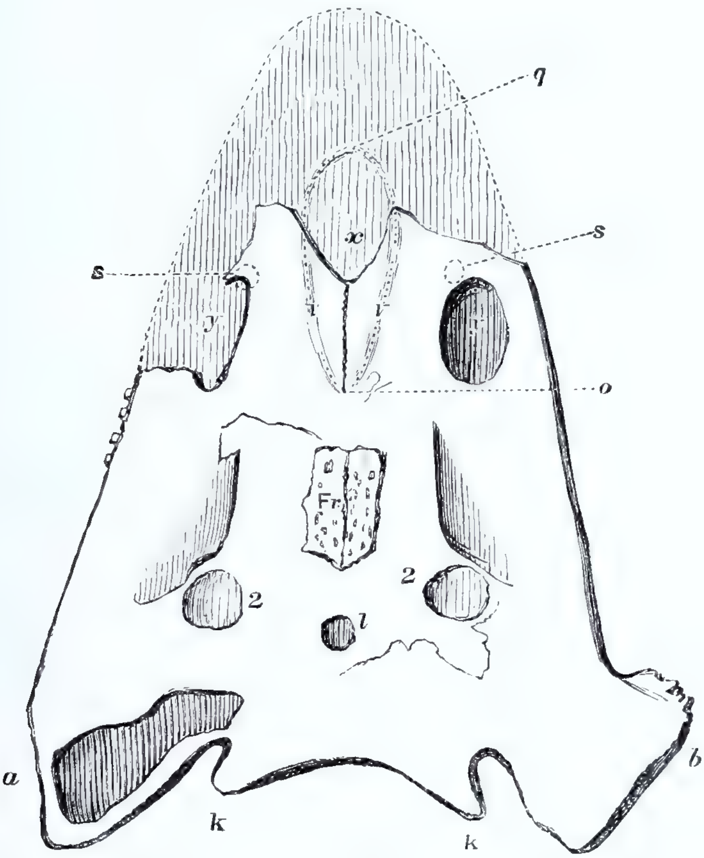


Fig. 2.

external nostrils (*s*), so as to show their relations to the apertures exhibited by the upper face of the palate, and it will be seen that the external nares are situated just in front of the line of the anterior margins of the posterior nares. No vomero-palatine or other sutures can be detected.

The relations of *Dasyceps* to the Labyrinthodonts will be clear to those who will compare Fig. 1 with Quenstedt's figure of the inner surface of the cranial bones of *Mastodonsaurus robustus* (Die Mastodonsaurier im Grünen Keupersandsteine Würtembergs; 1850; Tab. 1, Fig. 1). With many differences, both *Mastodonsaurus* and *Capitosaurus*

approach *Dasyceps* in the posterior situation and small size of their orbits, but the latter differs from these and from all other Labyrinthodonts with which I am acquainted, in the backward position of the external nostrils, in the existence of a "facial fontanelle,"[1] and in the magnitude and backward extension of the anterior palatine foramen. Add to these the characters of the teeth; the great size and posterior projection of the processes *k*, and the peculiarly rugose and almost spinulose sculpture of the surface of the cranial bones, and the generic distinction of *Dasyceps* from all other Labyrinthodonts appears to be fully justified.

The only other known Permian Labyrinthodont is the *Zygosaurus lucius* from the Cupriferous Zechstein of Russia, described by Eichwald in the "Bulletin de la Société Impériale des Naturalistes de Moscou," for 1848. It differs very widely from *Dasyceps*.

[1] This fontanelle would seem to correspond with the interspace left between the ascending processes of the premaxillary bones in the common frog.

XIV

ON A FRAGMENT OF A LOWER JAW OF A LARGE LABYRINTHODONT FROM CUBBINGTON

Memoirs of the Geological Survey of the United Kingdom, 1859, *pp.* 56—57.

THE original specimens of the large Labyrinthodont discovered by Dr. Buckland at Guy's Cliff, and described (from casts) by Prof. Owen under the name of *Labyrinthodon Jaegeri*, are, it would seem, lost; it is therefore fortunate that one of the collectors of the Survey, Mr. Richard Gibbs, has obtained from the quarry at Cubbington, whence other Labyrinthodont remains have been obtained, a fragment of a mandible which must have equalled, if it did not surpass, in size the so-called *Labyrinthodon Jaegeri*.

This fragment consists of about $7\frac{1}{2}$ inches of the hinder part of the left ramus of a lower jaw, exhibiting the articular cavity and the coronary edge in a good state of preservation, while the lower margin is somewhat fractured, and the posterior extremity is broken away.

The articular cavity is $1\frac{1}{8}$ inches long by $\frac{2}{3}$ of an inch wide, concave from before backwards, slightly convex from side to side. Its posterior margin rises into an abrupt transverse ridge, while its anterior limit passes gradually into the coronoid edge. The anterior end of the fragment measures $3\frac{1}{2}$ inches in depth, and this measurement must nearly coincide with that of the jaw when perfect. The posterior part of the suture between the angular and the articular elements of the mandible is well displayed, as is the remarkable, strong process sent off inwards and upwards by the former bone.

The outer surface of the angular bone is deeply ridged and grooved, the sculpture appearing to radiate from a point situated near the lower margin of the bone and $3\frac{1}{2}$ inches in front of the line of the posterior edge of the articular cavity. Towards the upper or coronary

edge of the ramus the pointed hinder extremity of the dentary bone is seen extending a little behind the level of the centre of radiation of the sculpture.

I may observe that this and other Labyrinthodont mandibles which I have seen show that each ramus was composed of only three elements, a dentary, an angular, and an articular, the last being continued forwards along the upper and inner side of the ramus, nearly to the symphysis, and thus taking the place of a splenial bone. The posterior, inferior, and internal part of the angular element sends a strong process upwards and inwards, and between this process and the outer part of the bone the articular is wedged.

Judging by the proportions exhibited by other Labyrinthodont remains from the Warwickshire Trias, it is probable that the entire jaw of which this fragment formed a part was about 2 feet long.

It is questionable whether more than one species of Labyrinthodont has been found in the English Triassic rocks; and the most perfect remains which have been obtained belong not to the German *Mastodonsaurus* (Jaeger), but to the perfectly distinct genus *Labyrinthodon* (Owen), which has been erroneously confounded with it. It is therefore quite possible, and even probable, that the mandible which I have just described may have belonged to a *Labyrinthodon* of large size, and not to *Mastodonsaurus Jaegeri*, with which, apparently merely on account of their size, the Guy's Cliff specimens have been identified.

In conclusion, I would caution geologists who are unacquainted with what has been done by Von Meyer and Plieninger, and others, towards elucidating the nature of the Labyrinthodonts, against supposing that there is any evidence whatever to show that the Labyrinthodonts were frog-like animals. All the positive evidence tends to show, on the contrary, that they were similar in form to the *Urodele Batrachia*, the salamanders and newts.

XV

OBSERVATIONS ON THE DEVELOPMENT OF SOME PARTS OF THE SKELETON OF FISHES

Quarterly Journal of Microscopical Science, vol. vii., 1859, *pp.* 33—46.

THE following observations were made principally upon the Stickleback (*Gasterosteus leiurus*) in the summer of the present year. Some of them were briefly alluded to in my Croonian lecture "On the Theory of the Vertebrate Skull," delivered before the Royal Society on the 17th of June last, and will be more fully treated of hereafter: the rest have not yet been published.

1. *On the development of the tail in Teleostean fishes.*

The fact that at a certain period in the embryonic life of Teleostean fishes, the extremity of the chorda dorsalis or notochord is bent upwards, was discovered and its importance indicated by K. E. Von Bär, in his 'Untersuchungen über die Entwickelungs-geschichte der Fische' (1835), where he remarks, respecting the embryos of *Cyprinus blicca*—

"I was greatly surprised to observe, that from the fifth day onwards, the posterior extremity of the vertebral column bends upwards, so that the caudal fin which now begins to be developed is not disposed symmetrically, but lies more below the extremity of the vertebral column; a relation which is permanent in the cartilaginous fishes." (p. 6.)

The conception of a relation between the embryonic condition of the tail in Teleostean fish and the adult state of the same organ in *Ganoidei* and *Elasmobranchii*, thus put forth, received a further development from Professor Vogt, the able author of the

'Embryologie des Salmones' (1842), which forms a part of M. Agassiz's 'Poissons d'Eau douce.' At p. 256 of this excellent monograph, Vogt says—

"The curvature of the extremity of the chorda dorsalis, which begins to be apparent in the *Coregonus* a short time before it is hatched, and attains its greatest amount about six weeks later, is another peculiarity of the embryos which deserves to be taken into consideration, because it subsequently disappears, and exists in adult fishes only in some genera of existing Ganoids and Placoids. These relations have not escaped the notice of observers, and M. Von Bär particularly expresses himself as follows."

Vogt here gives the preceding citation from Von Bär, and then continues :

"This peculiarity, together with many other features characteristic of embryos, has naturally led me to examine into the relations which exist between these modifications and the characters which distinguish the fossil fishes of different geological epochs. . . . . . It is a fact well known to all anatomists, that the vertebral column of cartilaginous fishes does not terminate in the same way as that of osseous fishes ; in the former the bodies of the vertebræ become successively smaller from before backwards, and incline upwards more or less towards the end of the tail, so that the part of the vertebral column which carries the rays of the caudal fin forms a very open angle with the longitudinal axis of the trunk. A very peculiar form of the caudal fin results from this disposition : instead of being symmetrically bifurcated, it is simply bilobed, in such a manner that the superior lobe, situated, like the inferior, under the prolongation of the vertebral column, extends further back than the latter, which is produced only by an elongation of the anterior rays of this same inferior side of the vertebræ. It results from this, that the caudal fin of the Plagiostomes has, properly speaking, no rays [1] inserted in the upper face of its vertebræ.

"In osseous fishes, on the other hand, the vertebral column terminates behind in a great expansion, whose superior and inferior apophyses are strongly dilated, so as to form a large vertical plate, whose posterior edge is symmetrically truncated, so as to present an equal surface of attachment for the caudal fin-rays above and below the prolongation of the vertebral column. This caudal piece may be regarded as resulting from many vertebræ soldered together, or else as a simple dilated vertebra carrying many vertical apophyses. The chorda dorsalis is continued in its interior, and is also a little

[1] This statement, however, is incorrect, as Müller had long before shown. (T. H. H.)

bent upwards, so that, neglecting the osseous vertebral rings which surround the chord, it terminates as in the Plagiostomes. But the apophyses of this caudal piece are always disposed in such a way that those of the superior face carry the upper half of the rays of the caudal fin, and the inferior apophyses the inferior rays; and the result is a very regular disposition of the caudal fin, which is divided into two equal lobes, whose rays are inserted like a fan upon the spinous processes of the last vertebra, and arranged in such a manner that the rays of the upper lobe correspond to the upper apophyses, and those of the lower lobe to the lower apophyses. The slight differences of form and size which are sometimes remarked between the two lobes never affect the disposition of the rays; for even when the caudal fin is cut square or rounded, it is not less invariably divided into two nearly equal parts, the superior of which is inserted on to the superior apophysis of the last vertebra. We may, then, regard this disposition as constant among osseous fishes, despite the slight inequality which is sometimes observed between the superior and inferior apophyses, and notwithstanding the curvature of the chorda at its posterior extremity."

M. Vogt then goes on to point out that since, according to M. Agassiz's researches, all fossil fishes before the Jurassic epoch had inequilobed or heterocercal tails, while those with equilobed or homocercal tails only appeared subsequently, there is a parallelism in this respect between the several stages of the embryo of such a (Cycloid) fish as a *Coregonus*, and the groups of fishes which have at successive epochs peopled the waters of the globe. In his 'Recherches sur les Poissons fossiles,' vol. ii, p. 102, the same doctrine is thus concisely expressed by M. Agassiz:

"On the other hand, there is neither in the actual creation nor in anterior epochs, any adult fish belonging to these two last orders (Ctenoids and Cycloids) which has the vertebral column bent up, and the caudal fin inserted below it; whilst this arrangement is characteristic of embryos in a certain period of their existence. There is then, as we have said above, a certain analogy, or rather a parallelism, to be established between the embryological development of the Cycloids and Ctenoids, and the genetic or palæontological development of the whole class."

Professor Owen ('Lectures on Fishes,' 1846) describes the caudal fin of the ordinary osseous fishes thus:

"The framework of the caudal fin is composed of the same intercalary and dermal spines superadded to the proper neural and hæmal spines of those caudal vertebræ which have coalesced and been

shortened by absorption, in the progress of embryonic development, to form the base of the terminal fin." (p. 67.)

It would be very desirable to know in what fish Professor Owen observed this singular process of coalescence and absorption. So definite a statement must rest on something more than mere supposition, and yet it is entirely unsupported by any hitherto published observations with which I am acquainted, and is, as will be seen below, directly opposed by my own.

In the excellent 'Lehrbuch der Vergeichenden Anatomie,' by Von Siebold and Stannius (1846), the latter ('Wirbelthiere,' p. 10) considers the vertical caudal plate to be produced by the coalescence of the superior and inferior arches, interhæmal and interneural bones "of the posterior caudal vertebra or of many of the caudal vertebræ ;" and in a note it is added, that the commencement of the process may be clearly traced in the pike.

A valuable paper published by the late eminent ichthyologist, Heckel, in the 'Sitzungs-berichte der Kaiserlichen Akademie der Wissenschaften' for 1850 (p. 143 et seq.), contained the first accurate and comprehensive account of the structure of the piscine tail, and threw quite a new light on the general doctrine of the relation between ancient and modern fishes.

"The few now-living successors of the bony Ganoids with complete vertebræ, which first appeared in the Jurassic period—our *Lepidosteus*, *Polypterus*, and probably also *Amria* (the latter of which I have had no opportunity of examining)—still have quite imperfect terminal vertebræ, behind which a part of the chorda persists in a perfectly unossified state. At the same time these terminal vertebræ appear to be developed in quite a different way from those of ordinary Teleosteans, for the arrested commencements of the posterior caudal vertebræ, or their first centres of ossification, appear, not as in the latter, above and below at the base of already formed spinous processes, but at the sides of the chorda, before either spinous processes or vertebral arches are developed. They become thickened anteriorly, and penetrate like wedges towards the axis of the chorda. Indeed, it would seem, from the fact that different individuals of these fishes, without distinction of size, present a considerable variation in the number of their terminal vertebræ (which may be even perfectly developed) as if they constantly added new vertebræ, whereby the end of the vertebral column—that is to say, the still naked chorda—must gradually, if not perfectly, be converted into ossified bodies of vertebræ. . . . . ."

"Another group of fishes, or rather of the now-living *Teleostei*

(whose origin is wrongly placed in the Cretaceous period, since it certainly took place much earlier, in the Jurassic epoch), also possess an imperfect vertebral column. No inconsiderable portion of the end of the chorda remains without developing vertebræ throughout the whole life of the fish, and becomes hidden under a roof-like arrangement of peculiar bones, which, supported upon the penultimate vertebral bones and projecting backwards beyond them, and seeming to be mere upper spinous processes, or ray bearers, unite with the broad inferior spinous processes which have coalesced so as to form a vertical fan-like plate. In these, as well as in the bony Ganoids mentioned above, the canal for the spinal cord, so soon as the vertebræ cease, passes back above the undivided chorda, and both are invested by a common case of solid cartilage, which takes the form of a long cone. It is a further peculiarity of the *Teleostei* in question, whose caudal rays, with the exception of the upper short ones ('stützen strahlen'), are altogether beneath the vertebral column, that their terminal vertebra is biconcave. The vertebral arches unite in pairs, and form by their proper elongation a double spinous process. In one part of these fishes (whose ancestors made their appearance in the Jurassic epoch) the arches are wedged into pits in the bodies of the vertebræ (as in *Thryssops*, *Tharsis*, *Leptolepis*, *Chirocentrites*, *Elops*, *Butirinus*, *Salmo*, *Coregonus*, *Saurus*, *Sudis*, *Esox*, *Umbra*). In the others, which only appear subsequently in the Chalk, the vertebral arches, and even the roof-like bones, are inseparably united with the bodies of the vertebræ (*Clupeidæ*, *Cyprinidæ*, *Cobitis*).

"In the great multitude of the remaining *Teleostei*, the end of the vertebral column is far more developed. The chorda is ossified to its extreme end, or crystallized into vertebræ, the last of which, therefore, possesses only a single funnel-shaped cavity, containing the end of the chorda, and turned forwards. But in the greater number of these Teleostei, whose ancestors made their appearance contemporaneously with the second division of the first-mentioned roof-tailed fish in the Chalk, the spinal canal alone is prolonged behind the last vertebral arches, as a bivalve or tubular bony sheath, between the fin-rays. These are the *Percidæ*, *Scorpænidæ*, *Sciænidæ*, *Chromidæ*, *Sparidæ*, *Squamipennes*, *Teuthidæ*, *Labyrinthiformes*, *Scombrædæ*, *Pæciliæ*, *Characinæ*, *Mormyridæ*, *Siluroidei*, and others. The smaller number began to exist an epoch later, with the tertiary formations, and in these only does the spinal marrow end at the same time with the chorda in the last vertebral body, or at least in an inseparable process of it (*Labridæ*, *Gadidæ*, *Blenniidæ*,

Gobiidæ, Pediculoti, Pleuronectidæ, Lophobranchii, Plectognathi, and others)."

I have omitted Heckel's account of the vertebral column of the Pycnodonts which precedes the long and important extract here given, as less immediately germane to the present subject. Suffice it to say, that he admits altogether three modes of termination of the chorda dorsalis: 1. The end is naked or unprotected by any ossification, as in Palæozoic Fishes and existing *Ganoidei*. 2. Its unossified end is protected to a greater or less extent by lateral roof-like plates, as in the *Salmonidæ*; these Heckel calls *Steguri*. 3. The end of the chorda is enclosed within the anterior cavity of the body of the terminal vertebra, as in the *Percidæ*, &c.

I shall bring forward grounds for believing that Heckel is mistaken as to this third mode of termination, and that in these fishes the end of the chorda really extends far beyond the anterior cavity of the last vertebra.

In 1854, Stannius published (as a part of the new edition of the 'Handbuch') his 'Zootomie der Fische,' beyond all comparison the best and most exhaustive work on the subject which has yet appeared. The structure of the fish's tail is discussed at p. 29, but very unaccountably all mention of Heckel's researches is omitted. In the *Blennidæ, Ophiodini, Tænioidæ, Murænoidæ, Fistulariæ*, the last caudal vertebra is said to end in a slight point. In *Cyclopterus, Callionymus*, the *Pleuronectidæ*, and *Plectognathi*, "the end of the last vertebra becomes flattened and slender, and is prolonged into a vertical broad plate, consisting of two quite symmetrical halves, an upper and an under."

A more detailed (but otherwise essentially similar) account to that of Heckel, of the tail of the *Salmonidæ*, is next given, and the like structure is said to obtain throughout life in the *Ganoidei*, in *Esox, Hyodon*, &c., while it is transitory in *Cyprinidæ, Characinæ*, and others.

In conclusion, Stannius points out that "many fish which pass for homocercal, show unmistakable traces of original heterocercality."

Having verified Stannius's account of the structure of the caudal extremity in the salmon, but seeing no reason to doubt—what was generally admitted—that other Teleostean fish were truly homocercal, I pointed out, in 1855,[1] that the foundation of the doctrine of Vogt and Agassiz was thereby destroyed. For Vogt's observations were made on a salmonoid fish, and a right comprehension of the structure of the tail in such fishes showed, that so far from the

[1] Friday evening meetings of the Royal Institution.

heterocercal tail of the embryo becoming homocercal in the adult, the tail of the latter was extremely heterocercal, far more so than that of many cartilaginous fishes. In fact, all that Vogt had really shown was, that the primitively homocercal tail of the embryo becomes gradually more and more heterocercal ; and he and others had been misled by the apparent homocercality of the adult fish into supposing that the heterocercality became lost again, whereas, in point of fact, it was only disguised.

Consequently, Vogt's observations did not prove in the least that a truly homocercal fish ever passed through a heterocercal state ; and as no observations respecting the development of the tail in what were supposed to be truly homocercal fish were extant, the doctrine that heterocercality precedes homocercality in embryonic life, was clearly not proven. On the other hand, until the development of some admitted homocercal fish had been examined, it was not disproved.

Having procured a number of very young sticklebacks and eels, which would assuredly be admitted to be true homocercal *Teleostei*, if such things exist at all, I gladly availed myself of the opportunity of examining into this point. I was not a little surprised to discover, not only that these fishes are heterocercal in the embryonic state, but that they are perfectly heterocercal in the adult condition, their apparent homocercality being, as in the case of the salmon and its allies, a mere disguised heterocercality.

In a Stickleback $\frac{5}{16}$ths of an inch long (fig. 1), I found the gradually tapering extremity of the notochord (*c*) bent upwards at a considerable angle with the axis of the body, and terminating close to the superior rounded corner of the caudal fin. In the greater part of its extent it was enclosed neither in cartilage nor in bone—though bony rings, the rudiments of the centra of the vertebræ, were developed in the wall of the notochord throughout the rest of the body.

The last of these rings (*b*) lay just where the notochord began to bend up. It was slightly longer than the bony ring which preceded it (*a*), and instead of having its posterior margin parallel with the anterior, it sloped from above, downwards and backwards. Two short osseous plates (*e*), attached to the anterior part of the inferior surface of the penultimate ring, or rudimentary vertebral centrum, passed downwards and a little backwards, and abutted against a slender elongated mass of cartilage (*g*). Similar cartilaginous bodies occupy the same relation to corresponding plates of bone in the anterior vertebræ in the region of the anal fin ; and it is here seen,

that while the bony plates coalesce and form the inferior arches of the caudal vertebræ, the cartilaginous elements at their extremities become the interhæmal bones. The cartilage connected with the inferior arch of the penultimate centrum is therefore an "interhæmal" cartilage. The anterior part of the inferior surface of the terminal ossification likewise has its osseous inferior arch (*f*) but the direction of this is nearly vertical, and though it is connected below with an element (*h*) which corresponds in position with the interhæmal cartilage, this cartilage is five or six times as large, and constitutes a broad vertical plate, longer than it is deep, and having its longest axis inclined downwards and backwards. Its superior and inferior margins are slightly excavated, the posterior is convex, the anterior deeply notched, so as to be divided into two processes, the anterior of which abuts against the inferior arch of the vertebra, while the posterior is applied against the posterior moiety of its under surface. On each side of the posterior convex edge of the cartilage (which they a little overlap), I found five slender osseous styles (*k*), the rudiments of the inferior caudal fin-rays.

Immediately behind and above this anterior hypural apophysis (as it may be termed) is another (*i*) very much smaller, vertical cartilaginous plate, which may be called the posterior hypural apophysis, having nearly the form of a right-angled triangle, and closely applied by its hypothenuse to the under surface of about the anterior two fifths of the free portion of the chorda. On each side of the posterior edge of this cartilage are three fin-rays (*k*), similar to those already described, so that in the caudal fin in this stage there are altogether eight double rays, and all these are inserted, not only below the notochord, but far in front of its termination.

No neural arch is as yet developed from the terminal osseous ring.

A great change had taken place in the tail of an embryo, *Gasterosteus*, $\frac{7}{16}$ths of an inch long (fig. 2). All the preceding parts, however, were readily recognisable, notwithstanding their modifications.

The penultimate centrum had become much longer in proportion to its thickness, its superior and inferior arches were much more developed, and the latter sent down a spine independently of the interhæmal cartilage, around which a sheath of bone, which had coalesced above with the posterior part of the inferior arch, was now visible. The anterior hypural apophysis had become longer in proportion to its breadth, and was coated with a thin layer of bone.

The posterior hypural apophysis had greatly enlarged both absolutely and in relation to the anterior, and traces of a bony deposit on its surface were discernible. The number of fin-rays had increased to fourteen ; of which two, very short, lay between the end of the interhæmal cartilage of the penultimate vertebra and the lower angle of the anterior hypural apophysis ; six, gradually increasing in length, and becoming jointed superiorly, embraced the posterior edge of the inferior hypural apophysis ; and six, of which the inferior were long and jointed at their ends, while the superior were simple styles, were connected with the posterior edge of the posterior or superior hypural apophysis. The terminal osseous ring (*b*) had in the meanwhile extended backwards, and now, as a slender tube, tapering posteriorly and obliquely truncated behind, embraced more than half the length of the previously free part of the notochord. As a consequence, the hypothenuse of the still triangular posterior hypural apophysis is now fixed to bone throughout its whole length, for the end of the bony sheath in question extends slightly beyond it. The remainder of the notochord (*c*) has its wall still membranous and unossified, and ends close to the superior and posterior angle of the caudal fin as before. There are no fin-rays above the notochord, nor is any neural arch developed from the terminal centrum, but the rudimentary interneural cartilage of the penultimate centrum had greatly elongated, and had taken the same position relatively to its superior arch as that occupied by the interhæmal cartilage relatively to the inferior arch, and had become surrounded by a sheath of bone. Behind this two other cartilages (*m*, *n*) lie parallel with one another above the ossified sheath of the chorda, but at present they are connected with no fin-rays. I will term these the "epiural" apophyses.

In a half-grown Stickleback (fig. 3) the anterior end of the terminal centrum was dilated and cup-like, just as if it were the anterior half of one of the ordinary hour-glass-like vertebræ, but instead of dilating again posteriorly, it is continued into a stout style, more than twice as long as the body of the penultimate centrum, and curved up so as to make an angle of 45° with the rest of the vertebral column. This stout style, with its central cavity, looks not very like the previous delicate sheath of the chorda; but such thickened sheath it really is, and with care the remainder of the notochord may be traced beyond it between two of the fin-rays into the tail-fin itself. The rays between which it lies are the uppermost of the superior set in the last-described embryo, and a new set, six in number, which have been formed above the noto-

chord. I shall henceforward term this ossified chordal style the "urostyle."

The free part of the notochord no longer reaches, by a long way, to the posterior superior angle of the caudal fin, for the fin-rays attached to the hypural apophyses, the uppermost of which supports the posterior superior angle of the caudal fin, are now more than twice as long as the free part of the notochord, and consequently the end of the latter is by its whole length distant from the present superior and posterior angle of the fin. The whole length of the free notochord, together with the elongated terminal centrum, is about 1-16th of an inch. The hypural apophyses are attached along the under surface of the ossified walls of the notochord. They are nearly equal in size, and each supports, as before, six rays, but the number in front of the anterior hypural apophyses has increased to six or seven.

A short and rudimentary neural arch rises from the anterior end of the urostyle, and there is an indication of a second opposite the interval between the anterior and posterior hypural apophyses, where I have seen traces of what seemed to be a sutural division of the urostyle into two portions.

The anterior epiural apophysis appears greatly enlarged and bifurcated at the extremity. I am inclined to think that its anterior part represents the neural spine of the anterior neural arch of the urostyle, but it is separated from it by a wide interval. The posterior epiural apophysis is also enlarged and altered in form.

In the adult fish (fig. 4) the urostyle is at once recognisable as a slender, tapering, bony process, in which an internal cavity can be observed, and which forms as great an angle with the axis of the vertebral column as before. The length of this process, together with that of the terminal centrum, of which it is a prolongation, is about 1-14th of an inch, and no trace of the notochord is visible beyond it, so that I doubt not it is the result of the complete ossification of the walls of the chorda. The posterior hypural apophysis is as nearly as may be of the same size as the anterior, and, like the latter, carries six large fin-rays. These almost entirely support the tail, the fin-rays above the notochord not attaining more than one fourth their length, and constituting only a very insignificant portion of the root of the tail. The epiural apophyses are greatly altered, but I need not enter into a particular description of them.

Thus it appears that *Gasterosteus* is in reality an excessively

heterocercal fish, the whole of its principal fin-rays being developed below the vertebral column. It is as heterocercal as an *Accipenser*, and far more so than a *Scyllium* or a *Squatina*. Furthermore it appears that the tail of this Acanthopteran fish has essentially the same structure as that of the Malacopteran salmon, except that the wall of the notochord is ossified through its whole extent, whereas in the salmon it persists in the condition which it has in the young *Gasterosteus*. I have not been able as yet to obtain so complete a series of forms of the caudal extremity in the Eel, but with some extremely interesting minor variations, which I propose to describe at length on a future occasion, the structure is similar in principle. The tail is truly heterocercal. What answers to the urostyle is divided into two portions—the anterior of which supports the anterior hypural apophysis, the posterior the posterior; and the last is not only superior to the anterior hypural apophysis, as is the case in the *Gasterosteus*, but projects beyond it posteriorly. Seeing the close resemblance in the structure of the tail which exists among all *Acanthopteri*—inasmuch as the hypural apophyses resemble more or less closely those of the stickleback, and always bear the principal caudal fin-rays, I make no doubt that what is true for *Gasterosteus* is true for all, and by a parity of reasoning, that what is true for *Anguilla* and *Salmo* is good for all *Malacopteri*; and I therefore do not hesitate to draw the conclusion that the *Ctenoidei* and *Cycloidei* of M. Agassiz, so far from being homocercal, are in truth excessively heterocercal; that is to say, more completely heterocercal than the great majority of *Elasmobranchii*.

In the heterocercal tails of the *Teleostei* there are, however, at least two well-marked varieties or grades of structure—the one, which might be called gymnochord tails, having the end of the notochord unprotected by ossification in its wall, as in the *Steguri* of Heckel; the other, which might be termed steganochord, having the end of the notochord enveloped in a styliform osseous coat, which there seems reason to believe represents the centra of two vertebræ. As a common, if not universal, character of the Teleostean heterocercal tail, by which it is distinguished from that of *Elasmobranchii*, we have the peculiar development of the epiural and hypural apophyses.

But if it be true that all Ctenoids and Cycloids are heterocercal, it is clear that the ground of the argument of MM. Agassiz and Vogt is completely cut away, so far as mere heterocercality goes. The ancient and the modern fishes are precisely on the same footing, and if the palæozoic *Ganoidei* and *Elasmobranchii* really represented

embryonic conditions of existing *Teleostei*, they ought to be all strictly homocercal, for it is only in the embryonic state that a Teleostean is really homocercal.

On the other hand, however, if homocercality and heterocercality are left out of the question, there can be no doubt that such facts as those brought forward by Heckel respecting the Pycnodonts show that in certain families of fish, at any rate, there has been a gradual change from a quasi-embryonic condition of the vertebral column to one more resembling that of an adult Teleostean. So perhaps it may be admitted that the structure of the tail in some modern Ganoids is more like that of the adult *Teleostei*, while that which obtains in the ancient members of the same group is more like that of embryonic *Teleostei*. But it has never yet been shown, either that the approximation of a Ganoid to a Teleostean, or the more complete ossification of the vertebral column in these or other fishes, is a mark of an advance in general organization. I take this occasion of repeating an opinion I have often expressed, that no known fact justifies us in concluding that the members of any given order of animals present, at the present day, an organization in essential respects more perfect (in whatever sense that word may be used) than that which they had in the earliest period of which we have any record of their existence.

It may be asked, in conclusion, whether the peculiar structure of the tail of the Teleostean tribes is a modification of the vertebral column altogether peculiar to them, or whether some trace of it is not to be found in other *Vertebrata*. I believe the latter question may be answered affirmatively, and that just where so many remnants of piscine characters are found, viz., in the *Amphibia*, there is a most interesting representation of this structure. I refer to the coccygeal style of the Frog and its allies, which, as Dugès originally indicated (and I have had reason lately to satisfy myself of the fact), is formed by the coalescence of a styliform ossification of the end of the sheath of the chorda with two neural arches. Naturally, as there are no fin-rays, there are no epiural or hypural apophyses, but otherwise the resemblance of the two structures is complete.

2. *On the development of the palato-pterygoid arc and hyomandibular suspensorium in Fishes.*

On examining the region in which the complex mass of bones comprehended under the above name eventually lies in an embryo *Gasterosteus*, about $\frac{1}{3}$d of an inch long, I found in their place a delicate inverted cartilaginous arch attached anteriorly by a very slender pedicle to the angle of the "facial cartilage" formed by the union of the two trabeculæ cranii, and posteriorly connected by a much thicker crus with the anterior portion of that part of the cranial wall which incloses the auditory organ. The crown of this inverted arch exhibits an articular condyle for the cartilaginous rudiment of the mandible. Its posterior crus is not, as it appears at first sight to be, a single continuous mass, but is composed of two perfectly distinct pieces of cartilage applied together by their respective anterior and posterior edges. The anterior is continuous below with the condyle, but ends above in a free point. The posterior is continuous with the cranial wall above, but ends below in a free point immediately behind the condyle. The posterior edge of this last portion (which I shall term the hyo-mandibular cartilage, as it is the means of suspension of both hyoid and mandibular arcs to the skull) has, above, a rounded condyle for the operculum, while below this, it gives attachment to that cartilage which eventually becomes the styloid element of the hyoidean arc. That part of the cartilage which lies above the attachment of this element becomes, by its ossification, the "temporal" of Cuvier; that which lies below it gives rise to Cuvier's "symplectique."

The anterior division of the posterior crus, the condyle, and the anterior crus of the inverted arch I have mentioned, constitute an inverted V-shaped "palato-quadrate" cartilage. The anterior part of the anterior crus ossifies, and becomes Cuvier's "palatine;" the posterior part gives rise to his "transverse" and "pterygoid;" the condyloid portion, when ossified, becomes his "jugal;" and the extremity of the ascending process from this or the anterior division of the posterior crus becomes his "tympanique."

The operculum, suboperculum, interoperculum, and preoperculum, are developed in the branchiostegal membrane apart from the other bones.

These embryological facts are of great importance, as they enable us to understand, on the one hand, the different modifications of the palato-suspensorial apparatus in fishes, and on the other hand, the

relations of the components of this apparatus to the corresponding parts in other *Vertebrata*.

They explain, in the first place, the fact to which Kostlin first drew attention, that in the Teleostean and Ganoid fishes there is every gradation, between the most intimate connexion of the "temporal" and "symplectic" with the other bones, and their wide separation. They enable us to understand why, in *Lepidosteus*, for example, the "jugal" remains firmly united with the representatives of the "pterygoid" and "tympanic," while it is connected with the "temporal" and "symplectic" only by the preoperculum; and they prove that the suspensorial apparatus of the sturgeon answers to the temporal and symplectic of other fishes, while the cartilaginous arch to which its mandible is articulated corresponds with the palato-quadrate arcade of the embryo. Again, to my mind, they prove that Cuvier was right in denying the homology of the so-called upper jaw of the *Elasmobranchii* with the maxilla and premaxilla of a Teleostean; for it corresponds precisely with the palato-quadrate arcade of the embryo, giving articulation to the lower jaw, which therefore is, as in the embryo, only indirectly connected with the so-called tympanic cartilage, which again is the homologue of the temporal and symplectic. In this respect, as in so many others where the skeleton is concerned, the Teleostean embryo is typified by the adult Elasmobranch and by some Ganoids.

With respect to the homologies of the bones of the fish's face in other vertebrata, the evidence of development appears to me to be no less decisive. No one who compares the development of the two will, I think, doubt that in the fish Cuvier's palatine is the homologue of the palatine of the abranchiate *Vertebrata*, that his pterygoid is the homologue of their pterygoid (wholly or in part), and that his jugal is their quadratum or incus. The comparison with the development of the frog, furthermore, leaves no doubt on my mind that the "tympanic" of the fish is a dismemberment of the pterygoid, and has not the remotest relation with the true tympanic. I can, however, find no homologue of the temporal and symplectic of the fish in the abranchiate *Vertebrata*. They appear to me to be specially piscine elements, which are only traceable as far as the *Amphibia*, where they are represented by that part of the suspensorial cartilage (quadrate or tympanic cartilage of authors) to which the hyoid arch is attached, and by the "temporal" of Cuvier. In the abranchiate *Vertebrata*, if the hyoid is connected with the skull at all, its insertion is quite distinct from that of the mandibular arch. I believe, therefore, that the branchiate *Vertebrata*, the oviparous

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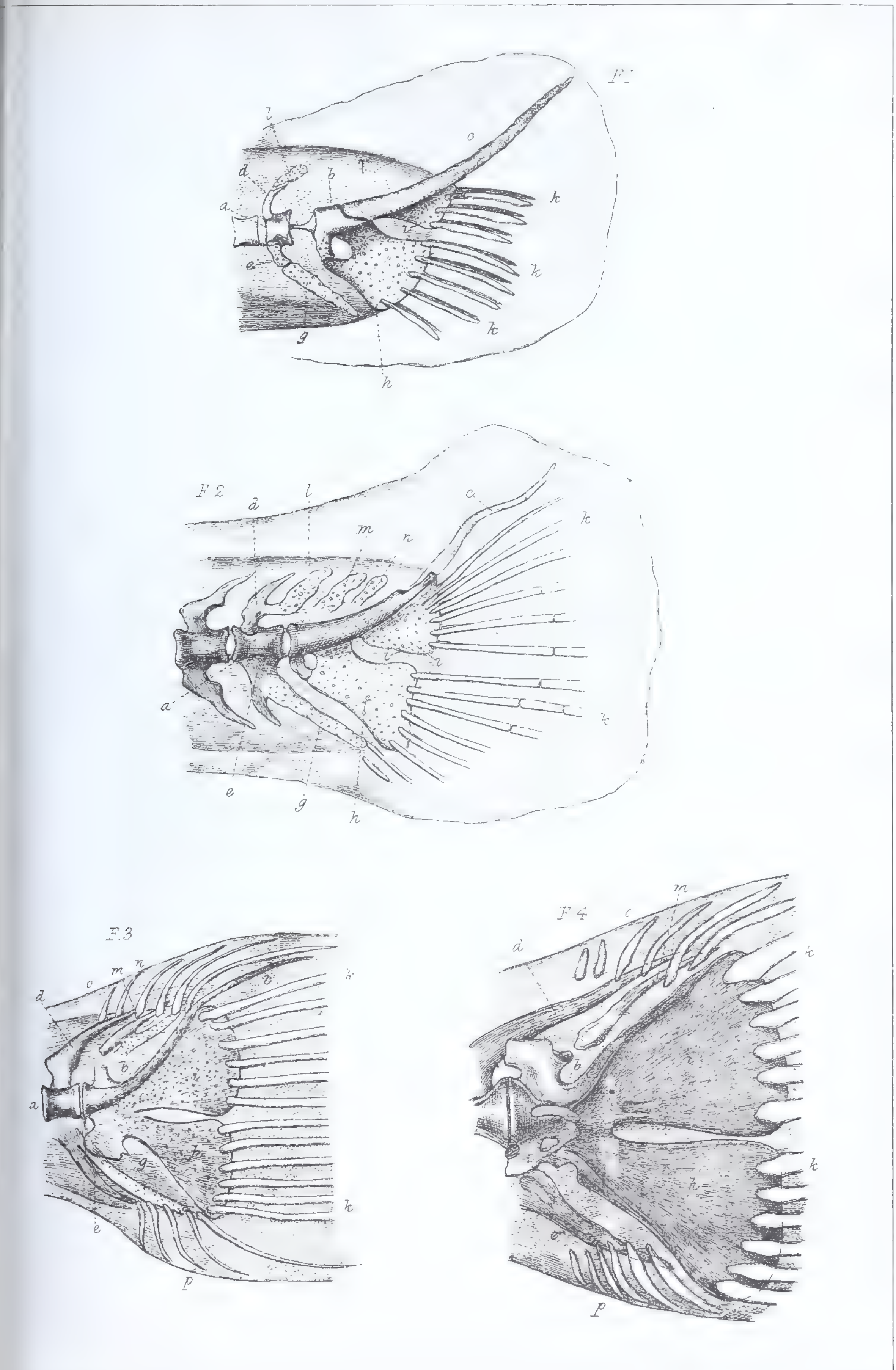

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abranchiate *Vertebrata*, and the *Mammalia*, present a series of well-marked gradations in the mode in which the ramus of the mandible is attached to the skull. In the fish it is separated by the os articulare, the quadratum, and the temporo symplectic. In the *Amphibia* the latter becomes less distinct. In the abranchiate *Ovipara* it disappears, but the ramus of the mandible is still separated from the skull by the articulare and quadratum. In the *Mammalia*, finally, these are converted into the malleus and incus respectively, and the ramus comes into direct contact with the squamosal element of the skull.

DESCRIPTION OF PLATE III. [Plate 28].

Fig. 1. The tail of a young fish, 5-16th of an inch long.
Fig. 2. The tail of a young fish, 7-16th of an inch long.
Fig. 3. The tail of a half-grown specimen.
Fig. 4. The tail of a full-grown *Gasterosteus*.

The two last figures are drawn in their proper relative proportions, while figs. 1 and 2 are on a much larger scale than figs. 3 and 4.

The letters have the same signification throughout.

a. Centrum of the last distinct vertebra.
b. Urostyle.
c. Notochord.
d. Neural arch of the last distinct vertebra.
e. Interior arch of the same vertebra.
g. Inter-hæmal cartilage or bone of the last ordinary vertebra.
h. Anterior hypural apophysis.
i. Posterior hypural apophysis.
k. Principal caudal fin-rays.
l. Interneural cartilage or bone of last ordinary vertebra.
m. Anterior epiural apophysis.
n. Posterior epiural apophysis.
o. Superior accessory fin-rays.
p. Inferior accessory fin-rays.

XVI

ON THE DERMAL ARMOUR OF *JACARE* AND *CAIMAN*, WITH NOTES ON THE SPECIFIC AND GENERIC CHARACTERS OF RECENT *CROCODILIA*.

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In the course of a recent investigation into the nature of the singular extinct reptile, *Stagonolepis*, I was led to inquire somewhat minutely into the character of the exoskeleton, or dermal armour, of the existing *Crocodilia*. To my surprise, I found that very little detailed information on this subject was to be obtained from the standard repertories of Comparative Anatomy, or even from the special monographs on Crocodilian structure and classification; but I was still more astonished to discover, among whole genera of recent *Crocodilia*, an exoskeleton possessed of characters such as have been universally supposed to be peculiar to long extinct forms of the order, and whose existence in any recent species has hitherto, so far as I can ascertain, been completely overlooked.

The attempt to discover the limits within which this remarkable exoskeleton is to be found, led me to look, more critically than I had previously done, into the arrangement and specific characterization of the recent *Crocodilia*. I have thereby arrived at results which, imperfect as they are, may be of service by leading others to inquire into the exact characters of species not at present within my reach; and I therefore propose to preface my account of the peculiarities of the exoskeleton in two of the genera of recent Crocodiles with some remarks on the classification of the group, and with a few notes upon the characters of the species and the limits of the genera.

Every one is acquainted with the great improvement effected in this branch of Herpetology by Cuvier, who divided the Crocodiles,

which he regarded as constituting only a single genus, into the three subgenera *Alligatores*, *Crocodili*, and *Longirostres*. Subsequent writers have admitted these highly natural subdivisions; but there has been a constant tendency to raise their rank. The genus *Crocodilus* has become the order *Crocodilia;* the subgenera *Alligatores*, &c., have been elevated into families; Dr. Gray has shown that the *Alligatores* must be divided into three genera, and that there are at least two genera of *Crocodili;* and, while one of Cuvier's species of *Longirostres* has been suppressed, the group is very generally retained with a changed name (*Gavialis*), a very important addition having been made to it in the *Crocodilus Schlegelii* of Müller and Schlegel.

Unless the considerable materials contained in the British Museum, the Hunterian collection, the collection of Dr. Grant, and the Christ-Church Museum at Oxford had been freely placed at my disposal, I should have been wholly unable to acquire the information contained in the following pages. It is only right, therefore, that I should take this opportunity of offering my thanks to my friends Dr. Gray, Prof. Quekett, Dr. Grant, and Dr. Rolleston for the many facilities they have liberally afforded me.

The recent species of the order *Crocodilia* are divisible into three families, which correspond with the original subgenera of Cuvier, and may be termed the *Alligatoridæ*, the *Crocodilidæ*, and the *Gavialidæ*.

I. In the ALLIGATORIDÆ the teeth are strong and unequal, and the posterior ones differ greatly in shape from the anterior. The anterior pair of mandibular teeth, and the fourth pair (or the so-called canines) are received into pits in the margins of the premaxilla and maxilla; while the mandibular teeth behind these pass inside, and not between, the maxillary teeth. The mandibular symphysis does not extend back beyond the level of the fifth tooth, and often not nearly so far. The line of the premaxillo-maxillary suture on the palate is straight, or convex forwards. The wide posterior nares look downwards, and are situated forwards on the palate.

This family embraces three genera, readily distinguishable by osteological characters—*Alligator*, *Caiman*, and *Jacare*.

Genus 1. ALLIGATOR.

Dental formula, $\frac{20-20}{20-20}$. 9th maxillary tooth the largest of its series. The snout is very broad, flattened, and rounded at the end. There is an indistinct longitudinal interorbital ridge; and there are two short ridges along the line of junction of the perfrontal and lachrymal bones. The aperture of the external nares is divided into two

parts, by the prolongation forwards of the nasal bones. The supra-temporal fossæ are well-marked and open, though not large. The vomers do not appear in the palate. The feet are well webbed. The dorsal bony scutes are not articulated together; and there are no ventral scutes.

This genus contains only one species, the well-known *Alligator Mississipiensis*, or *lucius*, which is exclusively North American.

Cuvier (Oss. Foss. ed. 4. vol. ix. p. 211) gives the appearance of the vomer in the palate as a general character of the *Alligatores;* but this bone is not visible in the palate of any of those *Alligatores* which Cuvier would have referred to his *A. lucius* or *A. palpebrosus*, and which form the genera *Alligator* and *Caiman* as here defined. The vomers are in fact as slender and delicate as in the Crocodile, and extend only between the level of the tenth maxillary tooth anteriorly and the descending processes of the prefrontal posteriorly.

What may be called the median nares, or the arch formed by the postero-lateral part of the vomer and the anterior and superior lamina of the palatine bone on each side (which would constitute the posterior boundary of the posterior nares, if the palatine and pterygoid bones gave off no inferior or palatine processes), are situated nearly on a level with the twelfth tooth, or with the palato-maxillary suture.

Genus 2. Caiman.

Dental formula $\frac{20-20}{22-22}$ (Natterer). The face is without median or transverse ridges, but it is sharply angulated along a line which extends from the orbit forwards along the sides of the snout. The anterior nasal aperture is undivided in the dry skull. The vomers do not appear in the palate. The supra-temporal fossæ are obliterated, the circumjacent bones uniting over them. The webs of the feet are rudimentary. The dorsal scutes are articulated together by lateral sutures and anterior and posterior facets; and there is a ventral shield, consisting of similarly articulated scutes.

Natterer[1] has described three species of *Caiman—C. palpebrosus*, *C. trigonatus*, and *C. gibbiceps*. The Caimans abound chiefly in tropical South America; but they are found as far north as Mexico, a specimen of *C. palpebrosus* in Dr. Grant's collection coming from that country.

[1] "Beitrag zur näheren Kenntniss der Sudamerikanischen Alligatoren," 'Annalen des Wiener Mus.,' Band i.

Genus 3. JACARE.

The snout is broad, and rounded at the end.[1] Each prefrontal bone is traversed close to its anterior extremity by the ends of a strong transverse ridge, which then curve round and pass forwards on the lachrymal and maxillary bones, to subside opposite the ninth tooth. The anterior nasal aperture is not divided by bone. The vomers, separated by a longitudinal suture, appear in the palate between the premaxillaries and the palatine plates of the maxillaries. The temporal fossæ, though not large, are open. The webs of the feet are small. The dorsal scutes are articulated together, as in the preceding genus; and there are similarly-articulated ventral scutes. There are 18—20 teeth on each side, above and below; and the fourth tooth in the upper jaw is the largest. The mandibular symphysis extends back nearly to the fifth tooth.

In a skull of *Jacare* (*fissipes?*), 19 inches long, in the British Museum, I find that part of the vomer which is visible in the palate to be a rhomboidal plate, somewhat truncated anteriorly, and rather more than $1\frac{1}{2}$ inch long and 1 inch wide. Its anterior end comes within $\frac{3}{8}$ths of an inch of the posterior margin of the anterior palatal foramen. Its posterior margin reaches to the level of the eighth tooth. The visible portion of each vomer is only its anterior end, which forms a thick and solid wedge-shaped plate, broader in front than behind, and articulating by a rough anterior and outer face with the premaxilla by an obliquely ridged posterior and outer face with the maxilla, and by its internal face with its fellow. Its upper, rounded surface projects but little into the nasal passage. $2\frac{1}{4}$ inches behind its anterior end, the posterior and upper extremity of the vomer passes into a thin and narrow plate of bone, whose plane is at first inclined at an angle of 45° to that of the anterior part of the bone, but gradually becomes vertical; as it does so it deepens until, 3 inches behind the anterior extremity, the vomer is a thin vertical plate of bone, $\frac{5}{8}$ths of an inch deep, which articulates below with the palatine plate of the maxilla, and, about 1 inch behind this, with the palatine plate of the palatine bone. The upper edge of this plate nowhere extends to one-third of the height of the nasal chamber. It gives off a horizontal process outwards, which, gradually increasing in width, inclines downwards until it comes into contact, first, with the inner surface of the maxilla, and, $\frac{3}{4}$ths of an inch behind this, with

[1] According to Natterer, the dental formula of *J. nigra* and *J. fissipes* is $\frac{18-18}{18-18}$, of *J. sclerops* $\frac{19-19}{20-02}$, of *J. vallifrons* and *J. punctualata* $\frac{20-20}{18-18}$.

the nasal plate of the palatine bone. In front of its junction with the maxilla, the horizontal plate of the vomer presents a long free edge, concave externally; and this bounds the median nares internally and posteriorly. Throughout its junction with the maxilla, the horizontal plate is parallel-sided; but after it joins the palatine bone, it gradually narrows posteriorly, in consequence of the gradual increase in width of the palatine, and ends almost in a point, $6\frac{1}{4}$ inches behind its anterior end. The posterior edge of the vertical plate is extremely thin, and $\frac{5}{8}$ths of an inch deep. It articulates with the anterior end of the vertical plate of the pterygoid, while the straight inferior edge articulates throughout with the palatine plate of the palatine bone. The vomers terminate midway between the median nares and the descending process of the prefrontal. The median nares are bounded entirely by the vomer and the maxilla. They correspond with the nasal face of the palato-maxillary suture, but are rather behind its palatine face, and they are about on a level with the interval between the tenth and eleventh teeth. If the anterior edge of the palatine bone bounded them, they would be a little behind the twelfth tooth. The posterior nares, $2\frac{1}{2}$ inches wide, by $\frac{7}{8}$ths of an inch long, look altogether downwards, are completely divided by a bony septum, and have the form of a rhomboid with its narrowest side posterior. They are surrounded by a strong raised ridge, incomplete only at the anterior and outer angles of the rhomboid.

Five species of *Jacare* are enumerated by Natterer—*J. fissipes*, *J. sclerops*, *J. nigra*, *J. punctulata*, and *J. vallifrons*. They have been met with only in South America.

II. In the family of the CROCODILIDÆ the teeth are usually strong and very unequal in size, and there is always a considerable difference between the anterior and the posterior teeth. The two anterior mandibular teeth are received into pits in the premaxilla; but the canines pass into grooves (which may be converted into fossæ) situated at the junction of the premaxilla and maxilla. The other mandibular teeth are received between the maxillary teeth. The symphysis of the lower jaw does not extend beyond the level of the seventh or the eighth mandibular tooth. The premaxillo-maxillary suture may be either straight or strongly convex backwards. The divided vomers do not appear in the palate. The posterior nares look more or less backwards, and are transversely elongated. The supra-temporal fossæ are always open, and the feet are distinctly webbed. The dorsal scutes are not articulated; and there are no ventral scutes.

Two genera, *Crocodilus* and *Mecistops*, are distinguishable in this family.

Genus 4. CROCODILUS.

The teeth are always strong and very unequal, the strongest in the upper jaw being the tenth. The mandibular symphysis does not extend beyond the level of the sixth tooth. There are usually six cervical scutes, in two rows, or forming a rhomb, and separated by a distinct interval from the tergal scutes. There are 18 or 19 teeth above, and 15 below, on each side.

1. *Crocodilus vulgaris.*

As Cuvier has remarked, it is extremely difficult to find good distinctive characters for all the species of this genus. My first difficulty was to ascertain the precise characters of that species which has been misnamed *vulgaris*, inasmuch as I could find neither in the British Museum, nor in the Museum of the Royal College of Surgeons, any *authentic* skeleton or skull of this, the so-called Nilotic Crocodile. This difficulty subsisted up to the time that the chief statements contained in the present essay were laid before the Linnean Society; but since then I have been enabled, by Dr. Gray's permission, to examine the skull of a small stuffed specimen, brought to this country from Egypt by Sir Gardner Wilkinson, and to study the splendid entire skeleton of a *Crocodilus vulgaris* in the Christchurch Museum at Oxford, presented to that Institution by the gentleman who shot it on the Nile, and set up with great care under the auspices of my friend Dr. Rolleston, Lee's Reader in Anatomy and Curator of the Museum. Fortunately the entire skin has been preserved; so that this is the most complete record of the hard parts of any individual crocodile with which I am acquainted, besides being, so far as I am aware, the only authentic entire skeleton of *Crocodilus vulgaris* in this country. I subjoin the chief points of interest which I noted in my brief examination of this valuable specimen:—

	Inches.
The total length of the skeleton is	114
,, ,, ,, skull	16
Between the outer edges of the posterior ends of the quadrate bones	$8\frac{3}{4}$
From the snout to the middle of the canine notch	$2\frac{3}{4}$
Transverse diameter of snout opposite 10th tooth	$4\frac{7}{8}$
Long axis of orbit	$2\frac{1}{4}$
Short axis of orbit	$1\frac{5}{8}$
Interorbital space opposite the middle of the orbit	$1\frac{3}{4}$
Anterior edge of the orbit from end of snout	$10\frac{1}{2}$

	Inches.
Syncipital[1] area in length, about	$2\frac{1}{2}$
,, ,, in breadth anteriorly	$3\frac{3}{4}$
,, ,, ,, posteriorly	4
Supra-temporal fossæ, wide	$\frac{7}{8}$
,, ,, long	$1\frac{1}{8}$
Least width of parietal	$\frac{7}{16}$
Total length of mandible	$20\frac{1}{2}$
Its greatest depth	3
Length of cervical region (or anterior 8 vertebræ)	$10\frac{1}{2}$
,, dorso-lumbar region	27
,, sacral ,,	$3\frac{3}{4}$
Length of humerus	$7\frac{1}{2}$
,, ulna	$5\frac{1}{4}$
,, fore foot, extreme length	6
,, femur	$8\frac{1}{2}$
,, tibia	6
,, hind foot, extreme length	$9\frac{1}{4}$

From the above measurements it will be seen that the skull is somewhat slender. Behind the canine groove it widens to the tenth tooth, which is $5\frac{3}{4}$ inches behind the end of the snout. It retains about the same diameter to the twelfth tooth, and then slowly widens again,—a sudden increase in size, to the extent of half an inch, taking place opposite the posterior margin of the orbit, owing to the flanging-out of the jugal. On the whole, however, there is a slow and even increase in breadth, from the canine groove to the ends of the ossa quadrata. The nasal aperture is pyriform, its wider end being forwards, and its narrow posterior extremity, into which the pointed ends of the nasal bones project, attaining the level of the first tooth behind the canine groove.

On the left side there is only a pit for the reception of the anterior mandibular tooth, while on the right side this pit is converted into a complete foramen. On the upper face of the skull, the pre-maxillo-maxillary suture runs vertically upwards through the canine groove, and then passes obliquely backwards to a point 5 inches behind the end of the snout. The anterior part of this suture lies in a strong ridge, which is continued downwards and forwards on the premaxilla to the level of the fifth tooth, a groove separating it from the margin of the nasal aperture. Posteriorly this ridge dies away, but a curved irregular elevation, convex inwards, arises opposite the tenth tooth. It is wholly confined to the maxilla, not extending on to the nasals.

There is a distinct, rough, irregular elevation, bounded on its outer

[1] By this term I denote that squarish flat area bounded by the postfrontal and squamosal bones laterally, by the occiput posteriorly, and by a line joining the outer angles of the post-frontals anteriorly.

side by a sharp groove, which extends back to the orbit, on the lachrymal bone. The profile of the skull is convex as far as the posterior boundary of the nostril, and very slightly concave from that point as far as the twelfth tooth. It then passes back as a straight, slightly ascending line, only interrupted by the lachrymal ridge, to the margin of the occiput. The inferior margin of the maxilla is convex downwards as far as the canine groove, whose lower end is indicated by a deep sinuation. It then becomes convex again, the crown of the curve being at the ninth and tenth teeth, and its posterior end sweeping into a concavity whose summit is at the twelfth tooth. Behind this the edge of the maxilla is only slightly convex. The inferior contour of the jugal bone is very concave; but the articular end of the quadrate bone descends to the level of the edge of the ninth alveolus.

The orbits have a sort of heart-shape, their apices being turned forwards, and their more convex sides inwards.

The supra-temporal fossæ are half-moon-shaped, their straight sides being external and so inclined that, if prolonged, they would decussate upon a line joining the anterior margins of the orbits.

On the palatine surface of the skull, the premaxillo-maxillary suture runs backwards from the canine groove, as far as the level of the middle of the second alveolus behind the groove (or that of the seventh tooth), which point it reaches at about the junction of the middle with the inner third of the palatine plate of the maxilla. The suture then turns abruptly forwards until it reaches the level of the anterior margin of the alveolus of the sixth tooth, when it bends suddenly inwards to meet its fellow. The whole suture, therefore, has the form of a W. The vomers are completely hidden.

The posterior nares look downwards and backwards; their aperture is, from the incompleteness of the septum, single, and has a transversely elongated crescentic form. It measures $1\frac{1}{8}$ inch in width by $\frac{3}{8}$ths antero-posteriorly. The basi-sphenoid is seen for about $\frac{1}{8}$th of an inch on the base of the skull behind it, bounding the sides of the eustachian tube. The dental formula is $\frac{18-18}{15-15}$. The fourth and tenth teeth are largest in the upper jaw, the first and fourth in the lower. The eight posterior teeth on each side in the upper jaw, and the five posterior in the lower, have a marked constriction between the short crown and the fang of the tooth. There are deep interdental pits for the reception of the mandibular teeth between the third and fourth, and fourth and fifth teeth above, and between the succeeding teeth from the sixth to the thirteenth.

The hyoidean cornua are very strong curved bones, the chord of whose arc measures $3\frac{1}{2}$ inches. They are concave inwards, convex

outwards, concave posteriorly, convex anteriorly; they are flattened from side to side below, but they end above in subcylindrical styloid extremities.

In the ninth vertebra the neurocentral suture passes just above the base of the parapophysis; it traverses the parapophysis in the tenth and eleventh vertebræ, while in the twelfth the parapophysis suddenly rises to the root of the diapophysis, and the suture lies far below it. The centra of the dorsal vertebræ, as far as the thirteenth inclusive, have hypapophyses. The diapophyses of the ninth vertebra pass almost horizontally outwards, but are a good deal inclined backwards. In the succeeding vertebræ up to the fourteenth or fifteenth, the diapophyses are, in addition, inclined upwards, the upward inclination being most marked in the tenth, eleventh and twelfth vertebræ. From the fifteenth vertebra onwards, the transverse processes pass almost directly outwards, without either upward or backward inclination. The span of the transverse processes is greatest in the eighteenth and nineteenth vertebræ, in which the distance between the extremities of these processes is $7\frac{1}{4}$ inches, a length about equal to that of the longest vertebral rib.

The rib of the ninth vertebra is terminated by a single long and slender semicartilaginous process which does not unite with the sternum. Each of the vertebral ribs from the tenth to the seventeenth vertebræ inclusively, on the other hand, is united with the sternum, or its continuation, by two such semicartilaginous costal elements, which may be respectively termed sternal and lateral. The sternal elements of the ribs of the tenth and eleventh vertebræ are united with the sternum proper; those of the next five vertebræ are connected with its median backward prolongation, while those of the seventeenth vertebra are attached to the processes into which this prolongation divides posteriorly.

The sternal costal elements are very broad and flat, and though the lateral ones are less so, they are wide and expanded. The lateral costal pieces of the eleventh to the sixteenth vertebræ inclusively, give attachment to very large and flat, triangular, *processus uncinati*. Those of the twelfth are $3\frac{3}{4}$ inches long and $1\frac{3}{8}$ inch wide at their widest part. The transverse processes of the twentieth vertebra bear rudimentary ribs. The centrum of the thirteenth vertebra is $1\frac{3}{4}$ inch long, and the vertebra is $3\frac{3}{4}$ inches high from the lower edge of the centrum to the summit of the neural spine. The centra of the vertebræ retain nearly the same length to the twentieth caudal; but behind this vertebra they are shorter, as are the anterior dorsal vertebræ. The first caudal vertebra is provided with two styliform bones, which

represent the chevron bones of the other caudal vertebræ, but are not united below.

The dorsal scutes have the arrangement which has often been described. They are separated (except perhaps the median rows) by integumentary spaces, neither overlapping nor uniting by sutures; and there are no ventral scutes.

Among the osteological characters which have been detailed, the peculiarities of the tergal armour, the proportions of the skull, combined with the characters of the ridges upon its surface, and the form of the premaxillo-maxillary suture amply suffice to diagnose this species. Even in the small skull, only $5\frac{1}{2}$ inches long, lent to me by Dr. Gray, the characteristic features of the species are well exhibited, although age appears to give rise to many differences. Thus the posterior margin of the external nostrils does not extend so far back as in the adult, and the facial is smaller in proportion to the syncipital region, whose anterior and posterior transverse dimensions are very nearly equal. The orbits are proportionally larger, the interorbital space more excavated; and the outer straight margins of the supratemporal fossæ are parallel with the longitudinal axis of the skull. Still more important differences are visible on the palatine face of the skull. The premaxillo-maxillary suture reaches back, indeed, to the line of the seventh tooth; but it forms an even curve whose summit is in the middle line. The aperture of the posterior nares, again, has a totally different form from that which it assumes in the adult. It is somewhat heart-shaped, with its apex forwards, measures $\frac{1}{4}$ inch long by $\frac{3}{16}$ths at broadest, and looks altogether downwards, while its anterior margin is situated far more forward in the palate than that of the adult.

2. *Crocodilus biporcatus.*

This, the best-known Crocodile, is a very well-marked species, characterized (beside the peculiarities of its dermal armour) by a comparatively slender skull, similar in shape to that of *C. vulgaris*, and, like it, without any sudden enlargement immediately behind the canine groove; and by the strong ridge which arises on each lachrymal bone close to the anterior edge of the orbit, and is continued forwards on to the line of junction of the nasal and maxillary bones, so that the naso-maxillary suture traverses the axis of the ridge, and then curves outwards, descending towards the alveolus of the tenth tooth. The premaxillo-maxillary suture is W-shaped; and its salient angles reach backwards even to the level of the posterior margin of the seventh alveolus.

3. *Crocodilus Americanus* (*acutus*, Cuv.)

has the slenderness of snout (even more marked) and the form of the premaxillo-maxillary suture of the preceding species; but it is at once distinguished from this and all other Crocodiles (except *C. rhombifer*) by the marked longitudinal and transverse convexity of the middle of the face, which gives the profile a totally different aspect from that of the other species, which are flat or concave in this region.

4. *Crocodilus Journei*

is another unmistakably distinct and very remarkable species. The descriptions and figures given by Graves, Bory de St. Vincent, and Duméril and Bibron, of the unique specimen of this Crocodile in the Bordeaux Museum, would alone have compelled me to differ entirely from the view taken by Dr. Gray of the affinities of this species. These observers agree in stating that *Crocodilus Journei* has six cervical scutes, arranged as in the other Crocodiles, and, as Graves says, "separated by an interval of four inches" from the commencement of the tergal scutes, whence it is obviously impossible that it can be a *Mecistops*. But, in addition to this, I had the good fortune to find among the recent additions to that excellent osteological collection which Dr. Gray has gradually formed at the British Museum, the skull of a Crocodile obtained from a dealer in Paris, and labelled by him "Croc. de l'Orinoke." I at first imagined this Crocodile to be a *Mecistops*; but on careful investigation it turned out to be no other than the skull of a *Crocodilus Journei*, somewhat larger than the Bordeaux specimen, but as the subjoined measurements will prove, agreeing with it in all its proportions:—

	Inches.
Length from end of snout to end of ossa quadrata	$22\frac{1}{2}$
Breadth between outer margins of ossa quadrata	$9\frac{3}{4}$
,, at the level of the anterior margins of the orbits	$5\frac{1}{2}$
,, at the tenth tooth	$3\frac{1}{2}$
,, at the end of the snout	$2\frac{3}{4}$
,, of the interorbital space	$1\frac{3}{4}$
Length of mandibular symphysis	5

Now Duméril and Bibron expressly state that the length of the head of *C. Journei* equals $2\frac{1}{2}$ times its greatest transverse diameter, that the width of the jaws at the anterior margins of the orbit equals one-fourth the length of the head, and that at the tenth tooth it equals one-sixth the length of the head; and these are as nearly as possible,

it will be observed, the relations of the same dimensions in the above list.

In the specimen in the British Museum there are eighteen teeth on each side above, and fifteen below. The Bordeaux specimen is stated to have the same dental formula, except that there are sixteen teeth in the left ramus of the mandible. The fourth and tenth maxillary teeth are stated by Graves to be as large again as the others; and the corresponding alveoli have these proportions to one another in the British Museum specimen. In fact, there can be no doubt that this skull is that of a true *Crocodilus Journei.*

But its general characters at once prove the close affinity of *C. Journei* with the other true Crocodiles, from which it differs only in its elongated and gradually tapering skull, and in the more backward extension of the mandibular symphysis,[1] which attains the level of the posterior margin of the sixth tooth.

In this character, and in the extreme slenderness of the snout, there is doubtless an approximation to *Mecistops*; but *Crocodilus Journei* is sharply separated from that genus by the characters of its teeth, and by those of its dermal armour.

5. *Crocodilus bombifrons* (*palustris ?*).

All the species of *Crocodilus* which I have hitherto mentioned have, in common, the backward curvature of the premaxillo-maxillary suture to the level of the seventh tooth. But there is a species of Crocodile, about whose proper specific name I am by no means clear, in which this suture passes straight across the palate, or may even be a little convex forwards.

And not only do the skulls of this species exhibit this approximation to those of the *Alligatoridæ*, but they resemble them still further in their rounded snouts, their great width immediately behind the canine groove, and in the fact that, in young specimens, one or the other canine may be received into a pit instead of into a groove.[2]

In the Hunterian Collection there are seven skulls, varying in

[1] The greater proportional length of the symphysis is noted by Duméril and Bibron.

[2] In a skull of this species $14\frac{1}{2}$ inches long, in the British Museum, the vomers are completely excluded from the palate, and their anterior ends do not extend for an eighth of an inch beyond the palatine part of the palato-maxillary suture, which lies on a level with the anterior margin of the twelfth alveolus. Each vomer is $2\frac{3}{8}$ inches long, and presents the same general form as that of *Jacare*; only the anterior division is but a very small, flat and thin plate, not a quarter of an inch long. The boundary of the median nares is formed in equal proportions by the vomer and the palatine, and is opposite the fourteenth tooth. The hinder end of the vomer articulates with the end of the descending process of the prefrontal.

length from $5\frac{1}{4}$ inches up to 16 inches, in none of which does the crown of the premaxillo-maxillary suture extend beyond a line joining the sixth pair of teeth. In all there are two short ridges (convergent in young specimens, nearly parallel in old ones) upon the lachrymal bones, which end before reaching the anterior limits of those bones. They all have an oblique ridge on the upper jaw above the tenth tooth; and the snout attains the width which it has opposite this tooth immediately behind the canine groove. In the British Museum there are five middle-sized skulls with the same characters; but two of these have a pit on one side of the upper jaw, and a groove on the other, and one has something between a pit and a groove on each side.

Dr. Gray has in his "Catalogue,"[1] mentioned the peculiar transverse disposition of the premaxillo-maxillary suture in his *Crocodilus bombifrons*; and on examining the two crania thus named in the British Museum collection, one of which is 20 and the other 21 inches long, I can discover no distinguishing character between them and those already described. There can be no doubt then, I think, that these constant and well-marked characters, exhibited by fourteen skulls which vary in length from $5\frac{1}{4}$ to 21 inches, prove the existence of a distinct species of Crocodile, which I would provisionally term *bombifrons*.

I believe that this species has been constantly confounded with *biporcatus*, from which it may be at once distinguished by the direction of the premaxillo-maxillary suture, and by the shape of the snout behind the canine groove. I have ound these distinctions to hold good at all ages; but the last-mentioned difference is far more marked in middle-aged than in either young or old specimens.

All the skulls named *Crocodilus palustris* which I have seen are referable either to *C. biporcatus* or to *C. bombifrons*. With respect to the *C. palustris* of Lesson and Duméril and Bibron, the latter authors consider it to be only a variety of *C. vulgaris*. Their description would, however, apply very well to *C. bombifrons*, as I have defined it above; and they expressly state ('Erp. Générale,' t. iii. p. 113) that all their specimens twelve in number and varying in length from 30 centimetres to more than 3 metres) came from the East Indies or the Seychelle Islands. Now, Duméril and Bibron enumerate only three Asiatic Crocodiles—*C. biporcatus*, *C. palustris*, and *C. galeatus*, the last of which was only known to them by description; so that all the numerous Asiatic crocodiles which passed through

[1] "Catalogue of the Tortoises, Crocodiles, and Amphisbænians in the Collection of the British Museum," 1844, p. 59.

their hands belonged either to *C. biporcatus* or *C. palustris.* On the other hand, all the skulls of crocodiles from Asia which I have met with (amounting to at least twenty) are either those of *C. biporcatus* or of the species which I have called *bombifrons*; so that I suspect the latter title will turn out to be a synonym of *palustris.*

6. *Crocodilus rhombifer.*

I have not been able to obtain any skull of this species, which, according to Cuvier's account and figures ('Oss. Fossiles,' t. ix. p. 102), resembles *C. Americanus* in the great convexity of its nasal region, but differs from it in the greater breadth of the skull, and in the strong converging preorbital ridges, which appear to be limited to the lachrymal bones. If the figures are to be trusted, however, there are other very important distinctive characters about the cranium of this species; for Cuvier's, fig. 2, pl. 331, which gives a view of the palate, shows the premaxillo-maxillary suture forming a nearly straight transverse line.

There remain several species of *Crocodilus* whose skulls I have not been able to examine, and of which no sufficient descriptions exist. Of these, (7.) *C. galeatus* and (8.) *C. Gravesii* (*planirostris*, would appear to be very distinct forms. (9.) *C. marginatus* is considered by Duméril and Bibron to be only a variety of *C. vulgaris*; and they take the same view of (10.) *Crocodilus suchus.* Professor Owen, however, has figured the cranium of an Egyptian mummy under this name ('Monograph on the Reptilia of the London Clay,' Pal. Soc. 1850). In the under-view of this skull (tab. i. fig. 2), the junction of the premaxilla and the maxilla in the palate seems to be broken away; but on the left side, the palatine process of the maxilla is entire, as far as the level of the anterior margin of the sixth tooth, and there is not a trace of a suture behind this point. Are there, then, two or more species of Crocodile in Egypt, as Geoffroy St.-Hilaire supposed?

With regard to the distribution of the species of *Crocodilus*, *C. vulgaris*, *C. marginatus*, and *C. suchus* (?) appear to be exclusively African; all the crocodiles from other parts of the Eastern hemisphere, which I have met with, belong, as I have stated above, either to *C. biporcatus* or *C. bombifrons*, both of which species are found in the Ganges. *Crocodilus galeatus* appears to be peculiar to Siam. *Crocodilus Americanus* and *C. rhombifer* are undoubtedly American. *C. Journei* has been supposed to be African; but such positive evidence

as exists tends rather to prove it to be an American species. Thus Bory de St. Vincent states that the Bordeaux specimen is "suspected to have come from America;" and, as I have said, the skull in the British Museum is labelled "from the Orinoko."

Crocodilus Gravesii (*planirostris*) is supposed by Bory de St. Vincent to have been brought from the Congo; but its real origin is not known.

Genus 5. MECISTOPS.

The cranium is elongated, and the snout slender and Gavial-like. There are eighteen slender and subequal teeth above, and fifteen below, on each side. The mandibular symphysis extends back to the level of the seventh tooth. The cervical scutes are arranged in two transverse rows, each of which contains two scutes; and there is no space left between the posterior row and the tergal series.

This excellent genus, as established by Dr. Gray, includes Cuvier's *Crocodilus cataphractus* (which Dr. Gray considers to be the young of a species whose full-grown form was discovered by Mr. Bennett in West Africa), *Crocodilus Journei* and *Crocodilus Schlegelii*. As I have endeavoured to show, however, *C. Journei* is a true crocodile; and, as I shall point out below, Müller and Schlegel have satisfactorily proved *C. Schlegelii* to be a Gavial. Consequently *Mecistops* is at present represented by only one species, which must be called *M. cataphractus* if *M. Bennettii* of Gray is really the adult of the form which Cuvier described.

III. In the family of the GAVIALIDÆ, the snout is always very long and slender; the teeth are for the most part slender, sharp-edged and subequal. The two anterior mandibular teeth pass into grooves, one of which lies on each side of a beak-like prominence of the premaxillæ, which carries the two anterior upper teeth. The canines are received into grooves. The mandibular symphysis extends back to at least the fourteenth tooth, and is partly formed by the junction of the splenial bones. The premaxillo-maxillary suture is always strongly convex backwards. The posterior nares are situated more forward than in the *Crocodili*. The temporal fossæ are large. The feet are strongly webbed. The dorsal scutes are not articulated; and there are no ventral scutes.

I distinguish two genera in this family, *Rhynchosuchus* and *Gavialis*.

Genus 6. RHYNCHOSUCHUS.

There are twenty teeth above, and eighteen or nineteen below, on each side; the mandibular symphysis extends to the fifteenth tooth.

The posterior teeth of the upper jaw, and almost all those of the lower jaw, are received into interdental pits; the orbital margins are not raised; and the premaxillæ are hardly at all expanded. The premaxillo-maxillary suture does not reach the third tooth behind the notch.

I propose the name *Rhynchosuchus* to indicate that generic type which is at present represented by the solitary species called by Müller and Schlegel *Crocodilus* (*Gavialis*) *Schlegelii*, and admirably described and figured by them in their essay, 'Over de Krokodilen van der Indischen Archipel,' in the 'Verhandelingen over de natuurlijke Gesch. der Nederl. overzee. Bezittingen,' 1839–1844. Under the title *Crocodilus* (*Gavialis*) *Schlegelii* (p. 18), they say—"The Gavial from Borneo, when compared with the Indian one, is principally distinguished by the following characters:—

"1. By its stronger form and better developed limbs.

"2. By its much less slender head and snout, which last does not narrow so suddenly in front of the eyes as in *G. Gangeticus*.

"3. By the smaller number of teeth, of which there are twenty above and eighteen below on each side, while *G. Gangeticus* has $\frac{28}{26}$ or $\frac{27}{25}$; furthermore, the teeth are stouter, less curved, and less sharp, and are disposed more perpendicularly, and the ninth tooth of the upper jaw (reckoning from the front) is considerably larger and stronger than the others; whence it follows that, just as in the true Crocodiles, the snout at the level of this tooth exhibits a lateral projection.

"4. By the shorter symphysis of the under jaw.

"5. By the absence of the swollen nasal prominence (neusklep), which characterizes the Gangetic Gavial.

"6. By the less expanded form of the tabular upper surface of the hinder part of the skull.

"7. By the very slight production of the edges of the orbit.

"8. By the large eyes.

"9. By the presence of a number of small nuchal shields, while *G. Gangeticus* has but one pair.

"10. By the strongly developed keels of the dorsal scutes.

"11. By the much larger scales on the under parts and on the legs of the animal.

"12. By the different colours with which it is variegated."

These authors further point out that the vomers appear for a small space in the posterior part of the palate, that the opercular or splenial bones join in the symphysis of the lower jaw, and that the cervical

and dorsal scutes form one continuous shield; and they represent the two anterior mandibular teeth passing in grooves on either side of the end of the premaxilla. In fact, they fully and completely establish the fact that their new species belongs to the *Longirostres* of Cuvier, or to the Gavials of later writers.

Under these circumstances, it is somewhat surprising to find the deliberate conclusions of these careful investigators set aside in the following brief passage:—

"This Bornean species (*C. Schlegelii*) was, in fact, originally described as a new species of Gavial; but the nasal bones, as in the fossil from Sheppey, figured in t. ii. 15, extend to the hinder border of the external nostril."—*Owen, Fossil Reptilia of the London Clay Crocodilia*, p. 15: 1850.

Müller and Schlegel give remarkably clear and beautiful figures of the skull of their Gavial; and these show at once that the nasal bones do not "reach the hinder border of the external nostril," but meet the premaxillaries at a point very distant from that border, viz. opposite the ninth tooth. Even did the nasal bones reach the posterior boundary of the nostril, such a character would not outweigh those derived from the relations and number of the teeth, the structure and extent of the mandibular symphysis, and the disposition of the dermal scutes,—all of which are so clearly and definitely set forth by Müller and Schlegel, that it seems difficult to understand how any one who had consulted the original memoir could have overlooked them.

It was possible, however, that Müller and Schlegel, notwithstanding their great opportunities, might have erred in their statements; and I therefore gladly seized the opportunity of testing their description by comparing it with an authentic skull of the species in question, from New Guinea, in the collection of the British Museum.

I have found the statement of Müller and Schlegel minutely accurate in almost all points; and there cannot be the slightest doubt, not only that the Schlegelian crocodile is one of the *Gavialidæ*, but that it forms a distinct generic type in that family, as different from *Gavialis* as *Caiman* is from *Jacare*, or *Mecistops* from *Crocodilus*.

The following are the most important measurements of the skull of *Rhynchosuchus Schlegelii* in the British Museum collection:—

	Inches.
Length from the end of the premaxilla to that of os quadratum...	23
Breadth from outer edge of one os quadratum to that of the other	8¾
Breadth aross the face in front of the orbits..........................	4

	Inches.
Breadth at the 9th tooth	2
,, at the 5th tooth	$1\frac{1}{2}$
,, at the 3rd tooth	$1\frac{3}{4}$
,, of the beak-like curved process which carries the two anterior teeth	1
Mean width of lower jaw from symphysis to extremity	$1\frac{5}{8}$
Length	12
No tooth measures transversely more than	$\frac{5}{16}$

The face is very smooth; but a slight longitudinal groove runs down on each side from the anterior margin of the orbit for about two inches. Anteriorly to this point the snout retains a nearly even diameter as far as the ninth tooth, in front of which it suddenly narrows a little, retaining nearly the same dimensions to the fourth tooth, where it widens a very little, and then suddenly narrows to the terminal beak. The lower jaw does not expand at all at its extremity. The nasals join the premaxillaries opposite the ninth tooth, and the splenial bones, in the lower jaw, end opposite the tenth mandibular tooth, as the figures of Müller and Schlegel show. The vomers appear between the inner edges of the palatines posteriorly, as a thin bony band $1\frac{3}{8}$ inch long by $\frac{1}{8}$ inch wide, which tapers at each end and is divided by a longitudinal suture. The ninth tooth of the upper jaw is stronger than the rest.

The only point in which the description of Müller and Schlegel seems to me to be incomplete[1] is with regard to the disposition of the teeth. They say—"The teeth of *C. Schlegelii*, as regards their form and development, more nearly resemble those of the true Crocodiles; but in the way in which the teeth of the two jaws are opposed, there is the most complete resemblance between our species and the Gangetic Gavial,—both which species differ from all other crocodiles in the circumstance that when the mouth is shut, all the teeth of the under jaw project outside the lateral margin of the upper jaw" (*l. c.* p. 22).

What I find is this:—The anterior teeth of both the upper jaw and the mandible are long, slender, sharp-edged, and slightly curved. The posterior eleven, on each side, in the upper jaw, are short, straight, conical, and constricted below their crowns. There are deep interdental pits between the ten posterior mandibular teeth, into which the opposed teeth of the maxilla are received when the jaws are closed. All the mandibular teeth, except the two anterior and the fourth pair, pass into like pits in the upper jaw. The anterior eight

[1] Or it is possible that the *Rhynchosuchus* from New Guinea, which I have examined, is specifically distinct from the Bornean form.

teeth on each side of the upper jaw pass straight down outside the lower jaw. In the Gangetic Gavial the relations of the teeth of the two jaws appear to me, as I shall state below, to be very different.

Rhynchosuchus Schlegelii inhabits the inland lakes of Borneo, and is found in New Guinea.

Genus 7. Gavialis.

There are twenty-seven or twenty-eight teeth in the upper, and twenty-five or twenty-six in the lower jaw. The mandibular symphysis extends to the twenty-third or twenty-fourth tooth. The lateral teeth of both jaws are, all but the very hindmost, directed obliquely downwards (or upwards), forwards or outwards, and are not received into interdental pits. The anterior margins of the orbits are raised. The premaxillæ and the end of the mandible are greatly expanded. The premaxillo-maxillary suture reaches the level of the fourth tooth behind the canine notch.

The only true *Gavialis* is the well-known *G. Gangeticus* from the East Indies. In this 'Gavial,' or 'Garrhial,' the vomers are slender bones which do not extend further forwards than the level of the twenty-second or twenty-first tooth, and have but a very short and slender representative of the anterior flattened division of the bone in *Jacare*; posteriorly they extend back to the level of the descending processes of the prefrontals. In a skull 25 inches long the vomers have a length of about 4 inches, extending as they do a little further forward than the palato-maxillary suture. The median nares are opposite the twenty-fifth tooth.

All the *Crocodilia* which I have enumerated are provided with two perfectly distinct kinds of dermal armour,—the one consisting of plates of horn, produced by a modification of the superficial layer of the epidermis; the other composed of discs of bone marked by a peculiar pitted sculpture on their outer surfaces, and developed within the substance of the dermis. To the former I shall apply the term "scales;" the latter are what I have denominated "scutes."

All recent *Crocodilia* have both scales and scutes in the dorsal region of the body, the scutes underlying, and having the same general form as, the scales. In all, the ventral region of the body is also covered with scales which have a very definite shape; but in no recent crocodilian which I have examined, save those species which are included in the genera *Caiman* and *Jacare*, are there any scutes in the ventral region.

Again, in the genera *Alligator*, *Crocodilus*, *Mecistops*, *Rhynchosuchus*, and *Gavialis*, the edges of the scutes, except those of the two median longitudinal rows, are hardly ever united by sutures, nor do the posterior margins of those in each transverse row overlap the anterior margins of the succeeding row. At any rate, there is no flat, bevelled, articular facet on the outer surface of the anterior margin of a scute, for articulation with the inner surface of the posterior margin of its predecessor. In the genera *Caiman* and *Jacare*, however, the lateral edges of all the scutes of the dorsal and ventral shields are united by serrated sutures; and the anterior end of the outer face of each is provided with a well-marked smooth facet, which is overlapped by the smooth under-surface of the scute in front of it.

I first noticed the remarkable structure of the dermal armour of these *Alligatoridæ* in the skin of a *Jacare* (*sp. incerta*), wanting the end of the tail, but which must have belonged to an animal between five and six feet in length. It had long been in my possession; but I had never before had occasion to study its characters minutely.

The horny scales, which had the appearance of thin tortoise-shell, could be readily peeled off (especially by the aid of a little caustic potash); and then the white surface of the subjacent bony scute upon which they were modelled came into view. It is to be understood, however, that the inner surface of the scale corresponded only in its general form with the outer surface of the scute; for it did not dip into the pits with which the latter is sculptured. These are in fact filled by the dry dermis which extends over and encloses the scute, a very thin layer (bearing the rete mucosum) being interposed between it and the scale; so that the pitted sculpture does not come out well until the scutes have been boiled.

The *dorsal* scutes are both carinated and angulated. By the application of the former term, I mean to indicate that, along a median or submedian longitudinal line, their substance is more or less elevated, so as, in many cases, to form a very prominent crest. This crest always subsides before it reaches the anterior margin of the scute, though it may extend beyond the posterior margin. Its highest point is always behind the centre of the scute, and is devoid of sculpture. The sculpture however seems to radiate from this point, inasmuch as it consists, on the greater part of the scute, of distinct pits, which are usually round towards the centre, but towards the periphery become ovals with their long axes directed towards the point in question.

The smooth inner surfaces of the scute shelve towards a depression

which corresponds with the external ridge, under which the sides of the scute seem to meet in an angle. This may be called the "angulation" of the scute. From before backwards, the inner surface of the scute is a little convex. The scute is thickest in the middle; posteriorly, it thins off to an edge and overlaps its successor; anteriorly, its outer surface is bevelled off at an acute angle with the inner, so as to give rise to a smooth shelving surface—wide from side to side, narrow from before backwards—forming the "articular facet," which is overlapped by the inner surface of the posterior edge of the preceding scute. I have termed this the "articular facet;" but it must not be supposed that there is anything like a true joint between the opposed facets of the overlapping and overlapped scutes; on the contrary they are at once separated and connected by the dermal connective tissue.

The posterior margin of the articular facet is separated by a deep transverse groove, divided by little partitions into as many pits, from the rest of the sculptured surface; but there is no trace of any suture dividing the scute into two portions. The lateral margins of each scute are united by serrated sutural edges with those which lie next to them in the same transverse row; so that each row forms a nearly solid flat bony bar, composed, in the middle of the back, of as many as ten distinct scutes. The outer edges of the outermost scutes only, thin off and exhibit no sutural serration, inasmuch as they are not directly connected with any other scutes.

The median line of the back corresponds in general with the suture between the two middle scutes of each transverse row; so that the scutes are disposed symmetrically on either side of that line. Furthermore, the anterior part of the inner surface of each of the two middle scutes is connected by ligament with the extremity of the spinous process of a vertebra; at least, this is the case in the dorsal, lumbar, sacral, and anterior caudal regions.

The scutes which protect the *ventral* side of the body, from the throat backwards, are four-sided and similar in their ornamentation to the dorsal scutes; but they exhibit neither ridge nor angulation, their outer and inner surfaces being parallel, and either nearly flat or evenly curved. Each forms, in fact, a segment of a large cylinder, inasmuch as the whole ventral shield is convex transversely, being nearly flat in the middle and much bent up at the sides. The dorsal shield, taken as a whole, is, on the contrary, nearly flat. The lateral edges of the ventral scutes interlock suturally; and their anterior and posterior edges are overlapped and overlap, just like the dorsal scutes. The

outer edges of the outermost ventral scutes thin off and are not united with any bony element; and the ventral, like the dorsal scutes, are usually arranged symmetrically on either side of the median sutural line. There may be as many as twenty-two scutes united by their lateral sutures into a single strong, curved, transverse, bony, bar-like segment of the ventral armour.

Throughout the neck and body, and as far as the commencement of the tail, the ends of the dorsal and ventral bony bars, whose sum may be regarded as a dorsal and a ventral shield respectively, are separated by an interval of integument, in which only small scattered scutes are visible. The physiological import of this arrangement becomes obvious when we consider in what manner the animal breathes; and indeed the integumentary interval answers very precisely to the leather which connects the two boards of a bellows. Again, though the limbs are themselves covered with articulated scutes, they are afforded free play upon the body by this flexible interspace. Immediately behind the hind legs, the ventral and dorsal shields unite; and the tail is from that point surrounded by a succession of bony hoops, each of which corresponds with a vertebra, the segments of the exo-skeleton answering to those of the endo-skeleton.

The most remarkable feature about the ventral scutes, however, and that in which they differ most widely from the dorsal ones, consists in the fact that each scute is composed of two distinct pieces, an anterior and a posterior, which unite together by a transverse serrated suture. The anterior piece or "semi-scute" may attain to three-quarters the length of the posterior, and it has exactly the same width. The anterior semi-scute bears the articular facet and the transverse pitted groove, whose posterior wall is just in front of its hinder edge, or in other words, of the suture, when the two semi-scutes are united.

Such are the general characters and mode of arrangement of the dorsal and ventral armour of *Jacare*. But there remain many noteworthy peculiarities in the disposition and number of the components of each band of the armour.

Thus, in the *dorsal shield* there are two rows of nuchal scutes, each containing eight separate keeled bony plates; and of cervical scutes there are five rows, the two anterior of which contain four angulated and carinated scutes each, while the three posterior contain only two scutes each. All these scutes, except the anterior row, have articular facets; and all those of each row are united suturally. Of dorsal scutes there are thirty transverse rows up to the median keel of the

tail, which commences with the thirty-first row. The number of scutes in each row is as follows:—

Rows.	Scutes.	Rows.	Scutes.
1, 2, 3, 4	6	25, 26	5
5, 6, 7, 8, 9, 10, 11	10	27, 28	4
12, 13	8	29, 30	4
14, 15	6		
16, 17, 18	4	31, 32, 33, 34	5
19	6	The rest of the tail is wanting.	
20	8		
23, 24	6		

Throughout the dorso-lumbar and sacral regions (*i.e.* up to the nineteenth row), the median scutes are hardly keeled at all, while the outer ones are the more strongly carinate the more external they lie.

In the caudal region, the second scute from the middle line, in the twenty-third row, has a strong keel and angulation, which grows stronger in the corresponding scutes up to the thirtieth inclusive, until the superior and lateral faces of these scutes, in the twenty-ninth and thirtieth rows, are inclined to one another at a right angle and very strongly keeled. I have said that, as a rule, the median line is occupied by a suture between two median scutes; but in the caudal region,[1] in the twenty-fifth row (which corresponds with the sixth caudal vertebra) the two median scutes are replaced by one flat scute, so that there is no suture in the middle line. In the twenty-sixth row there is a similar arrangement, but the flat scute is smaller; and in the twenty-seventh no trace of it is left, so that the strongly keeled lateral scutes meet in the middle line, which is again occupied by a suture. This continues up to the thirty-first row, when the median scute reappears as a thin vertical plate, broader below and in front, where it articulates with the median lateral scutes, than above and behind, where it exhibits a free edge only covered by the horny epidermis. It is thus that the serrated dorsal crest of the tail is formed. The scutes of the crest exhibit only very small round and distant pits.

The *ventral shield* begins in the neck just behind the level of the anterior margins of the orbits: the fifteen anterior rows may be termed subcervical, as they lie in front of the thorax. In the first six rows the scutes are very small, and increase in number up to twelve in a row. In the next six rows there are ten scutes in a row, and in the last three, twelve. All these rows are symmetrically divided by

[1] The second and third cervical rows in *Caiman palpebrosus* and *trigonatus* also contain a median scute, and consequently an odd number of scutes. In *Caiman trigonatus*, the third to the ninth supra-caudal rows have each a median single scute.

the median line. In the three hinder rows the inner scutes are longer than the outer ones; and this is most markedly the case in the fifteenth row, whose innermost scute is half as long again as the corresponding one of the preceding row, and more than three times as long as the outermost of its own row.

The sixteenth row differs from its predecessors and successors, and may be termed the axillary row. It is bent upon itself with an angle open forwards, and is divided into two halves (each of which contains seven scutes) by the union of the middle scutes of the fifteenth subcervical with those of the first row of what may be termed the subdorsal scutes, or those which lie under the thorax and abdomen. Of subdorsal and subcaudal scutes there are, up to the broken-off end of the tail, thirty-seven rows, with the following numbers of scutes:—

Rows.	Scutes.	Rows.	Scutes.
1	12	22	18
2	10	23	22
3, 4, 5	12	24	22
6, 7, 8, 9	14	25	20
10	16	26—28	18
11	14	29—31	16
12—17	14	32—34	14
18—20	12	35	12
21	14	36, 37	10

It will be noticed that there are three more rows of ventral than of dorsal scutes. On endeavouring to ascertain how this came about, I observed that the first subdorsal was a good deal behind the first dorsal row, though the eighth to the twelfth dorsal corresponded exactly with the eighth to the twelfth ventral rows. In the anterior part of the body, therefore, there is a clear general correspondence between the segments of the dorsal and those of the ventral armour.

In the caudal region, again, I found that the twenty-fourth ventral row, which is the first of the caudal rows not excavated by the vent, corresponded exactly with the twenty-first dorsal row. It was clear, therefore, that three ventral rows were interpolated somewhere between the twelfth and twenty-first dorsal rows; and on close examination I found this interpolation to arise from the doubling of the fourteenth, fifteenth, and sixteenth ventral rows.

I have examined *Jacare fissipes* and *nigra*, *Caiman trigonatus*, and *C. gibbiceps*, in the British Museum; and I find, in all, dorsal and ventral armour having the same essential arrangement as that just described. A specimen of *Caiman palpebrosus* about two feet long, the opportunity of examining which I owe to Dr. Grant, exhibits the dorsal and ventral shields (whose scutes are in the main similarly

arranged) very beautifully; and a young *Jacare* of about 18 inches in length, for which I am indebted to the kindness of the same gentleman, proves that the scutes are developed even in specimens of this age. I have no hesitation therefore in expressing my belief that this singularly complete dermal armour will be found to be characteristic of all the species of the genera *Caiman* and *Jacare*. On the other hand, I have examined *Alligator Mississipiensis*, *Crocodilus vulgaris*, *C. biporcatus*, *C. Americanus*, *C. rhombifer*, and *C. bombifrons*, *Mecistops cataphractus*, and *Gavialis Gangeticus*, of various ages and sizes, without having been able to discover a trace of ventral scutes. This is the more remarkable, as the well-marked ventral and dorsal shields of many of the ancient *Teleosauria* would lead one to expect a corresponding exoskeleton (if anywhere) in their nearest allies, the modern *Gavialidæ*. However, *Goniopholis*, with its strong armour, is more like an ordinary Crocodile; and I have recently discovered that a true Crocodile in some respects curiously similar to *C. bombifrons* (*C. Hastingsiæ*) was covered with scutes exceedingly like those of the modern *Caiman* and *Jacare*.

In minute structure the bony scutes of *Jacare* closely resemble those of such a fish as a Sturgeon: a middle layer, containing so many canals as to appear almost cancellated in longitudinal or transverse section, is covered externally by a thin, and internally by a thick, layer composed of bony lamellæ, nearly parallel to the plane of the scute. Round the canals of the middle layer, the bony lamellæ are disposed concentrically, to a greater or less extent. The lacunæ are of very various shapes; and there are perhaps as many short as elongated forms. The canals of the middle layer communicate by large branches with the inner, by smaller and fewer branches with the outer surface of the scute.

In the young *Jacare* mentioned above, I found the dermis to be distinguishable into two layers. The more superficial of these is thin, made up of irregular or formless connective tissue, and contains many ramified pigment-masses. Its smooth outer surface underlies the rete mucosum. Internally, it passes into the second or deep layer, which consists of successive layers of distinctly fibrous connective tissue, disposed in definite parallel bundles, and having a very regular arrangement. Throughout a space corresponding with the area of each scale, in fact, the bundles of each layer cross those of the succeeding layer at right angles; and the successive tiers of bundles are tied together by short cords disposed perpendicularly to the planes of the tiers. A corresponding arrangement of the bundles of connective tissue has long been known to obtain in the dermis of Fishes and

Batrachia. At each end of this small "mat" of connective tissue, the bundles, if I may so say, fray out; and at the anterior end, the layers, loosened in texture, bend upwards, spreading out at the same time to become continuous with the fibres of the "mat" in front. In consequence of the matting under the quadrate surface of each scale, the dermis has a peculiar facetted aspect, quite apart from any osseous deposit. Where bony scutes are formed, they appear as very thin perforated plates in the most superficial portion of the deep layer of the dermis; so that there is a single thin layer of dense connective tissue above them, while below them are all the rest of the denser and deeper lamellæ of the dermis. Through the apertures in this primitive osseous plate (the rudiment of the middle layer of the future scute), bundles of connective tissue extend, connecting the deep with the superjacent lamellæ.

If a thin section is made and decalcified with weak acid under the microscope, the calcareous matter, as it is dissolved away, leaves an obscurely fibrous matrix of a different aspect from the surrounding connective tissue, and the endoplasts, or nuclei, of this matrix are seen each to have occupied the centre of a lacuna.

Again, the rudimentary scute lies in the dermis as in a sort of pocket, the superficial and deep walls of which separate from it with great ease; and in good thin sections made through the dermis and scute, there seems to be no direct connection between the substance of the scute above and below, and the connective tissue with which it is in contact. Nor could I satisfy myself that the margins of the scute were continuous with the surrounding bundles of connective tissue. However, the specimen had been a very long time in spirit; and I am unwilling to lay too much stress upon these observations, which tend to negative the supposition that the scute proceeds from the direct calcification of the connective tissue of the dermis.

On the other hand, I must remark that horizontal sections of the scutes have presented oblique parallel fissures, sometimes crossing one another, which might readily be supposed to correspond with the lines of separation of ossified bundles of connective tissue.

NOTE.—During a recent visit to Paris, my friend Mr. Busk was kind enough to examine the specimens of recent *Crocodilia* in the Museum of the Jardin des Plantes, with reference to certain points to which I requested his attention. Mr. Busk informs me that there is no doubt about the transverse direction of the premaxillo-maxillary suture in *Crocodilus rhombifer*; and his statements lead me to entertain no question that *C. bombifrons* is a synonym of *C. palustris*.

In the typical specimens of *C. marginatus* and *C. suchus* of Geoffroy St.-Hilaire, the premaxillo-maxillary suture extends back to the level of the seventh tooth.

Mr. Busk has furthermore pointed out to me the existence of another American species of Crocodile—*C. Morelettii*, which has been described by M. Auguste Duméril in his "Description des Reptiles nouveaux ou imparfaitement connus," &c., 'Archives du Muséum,' t. vi. 1852.

This species inhabits lake Flores, in Yucatan; and it is said by M. Duméril to approach *C. Americanus*, from which it differs in the proportions of the skull and in the characters of the dermal armour.

June 21st, 1859.

XVII

ON THE ANATOMY AND DEVELOPMENT OF PYROSOMA.

Transactions of the Linnean Society of London, vol. xxiii., 1862, *pp.* 193–250.
(*Read December 1st*, 1859.)

§ 1. *History of the Genus* PYROSOMA.

THE genus *Pyrosoma* was first established in 1804 by Péron, in a memoir[1] published in the fourth volume of the 'Annales du Muséum,' and accompanied by a plate representing the exterior and a longitudinal section of the animal. Péron thus defines the genus and the species which he observed :—

"PYROSOMA.

"Corpus liberum, subconicum, extremitate ampliore apertum vacuum, aperturæ margine intus tuberculis cincto.

"PYROSOMA ATLANTICUM. Æquatorio-atlanticum, gregarie pelagivagum, viridissime phosphorescens, coloribus eximiis tunc effulgens, in aquis viginti duobus reaumurianis calidioribus occurrens, 10–12, 14–16 centrimetros æquans."

M. Péron's conceptions of the exigencies of a zoological diagnosis were evidently of a singular kind, and his memoir contains not a single observation calculated to throw light upon the true nature of one of the most remarkable animals that has ever been discovered.

[1] "Mémoire sur le nouveau genre *Pyrosoma*," par M. Péron. Annales du Muséum, tom. iv. p. 437, 1804.

Forskål's Descriptiones Animalium (1775) contains the following passage :—

"29. MEDUSA BEROË. Tres ejus varietates vidi vel species. * * * * *

"29*c*. RUFESCENS : ovato-oblonga ; sæpe 5 poll. longa ; intus prorsus vacua. Gallicè, *Concombre de la mer*. In mari Mediterraneo frequens."

Was *Medusa Beröe rufescens* a *Pyrosoma*?

With respect to the striking property which gave rise to the name conferred on the genus, Péron asserts that the *Pyrosomata* exhibited movements of alternate contraction and dilatation at regular intervals; and that each contraction was accompanied by the development of a luminosity, which, when at its brightest, was red, but, in dying away, passed through shades of orange, green, and blue. The light was developed upon irritation, and entirely ceased with the animal's death. The only indication of locomotive power was the regular contraction just described, whose necessary effect was a slight retrogressive movement, in consequence of the reaction of the water forced out of the open end of the *Pyrosoma*.

In 1815, Lesueur, having previously, as he states, described and figured a new species (*P. elegans*) in the 'Nouveau Bulletin de la Société Philomatique' for 1813, added a number of important details to Péron's account in his "Mémoire sur l'organisation des Pyrosomes, et sur la place qu'ils doivent occuper dans une classification naturelle,[1]" and showed that Lamarck was in error in assigning to *Pyrosoma* a place near *Beroë*, the animal being, in reality, a mollusk closely allied to *Salpa* (*l. c.* p. 420).

The species described by Lesueur was named by him *P. giganteum*, and was obtained in the Mediterranean, near Nice.

Pyrosoma giganteum, says Lesueur, has the general form common to the two other species; it is transparent, of a starchy blue colour, soft and gelatinous, though slightly coriaceous; its only aperture, placed at the upper end, is bounded by tubercles, and provided with a membranous expansion, which in certain cases serves to close it. The whole body is covered externally with tubercles, but these are not disposed regularly like those of *Pyrosoma elegans*; they vary in their dimensions, some being short and indistinct, while others are greatly developed. The largest are conico-cylindrical, flattened and lanceolate at the extremity (while those of *P. atlanticum* are simply conical), with a small aperture situated upon that side which looks towards the bottom of the sac: this lanceolate extremity is notched on its sharp edges, and presents below, between its pointed extremity and the opening of which we have just spoken, a small but very prominent keel. The inner surface of the *Pyrosoma* is smooth, and provided with a great quantity of little apertures, each of which corresponds with one of the tubercles, and is only the anterior end of a canal, whose posterior aperture is placed at the free extremity of the tubercle,—a fact easily demonstrated by pouring

[1] Read to the Société Philomatique de Paris on the 4th of March, 1815, and published in the 'Journal de Physique' for June of the same year.

water into the sac-like body of the *Pyrosoma* ; for the water passes out immediately, in a multitude of distinct jets, from the extremities of the tubercles.

Lesueur next proceeds to describe the internal structure of the *Pyrosoma.* He mentions the internal and atrial tunics as one internal tunic, and points out their distinctness from the external, except at the aperture and over those rounded lateral bodies, which I have much reason to think are renal organs. The branchial networks are recognized as such ; the endostyle is described as "un vaisseau replié sur lui-même ;" the testis is noted, but is interpreted as the liver. The stomach is determined as such, while the intestine is regarded as the œsophagus ; and the œsophagus is considered to be the pylorus, opening into what Lesueur regards as the intestine—"un canal assez large, glanduleux vers sa base" (p. 417), but which is, in reality, a sinus full of blood-corpuscles.

The peripharyngeal ridge is accurately described as "deux petits filets qui vont en se courbant de chaque côté," &c. (p. 419) ; and the nature of the nervous ganglion is rightly determined. *Pyrosoma* is classed among the compound organisms, and the fœtuses are carefully though briefly noted. Lesueur confirms Péron's statement concerning the rhythmical contractions exhibited by the whole body in the *Pyrosomata.*

The figures which accompany this memoir are exceedingly good. I judge from them that Lesueur observed the atrial muscles, and that he has mentioned them as the line which separates the first zone of his transverse section (fig. 13 *b*) from the second (p. 415) ; and again, in the description of the figures 5 & 6, as "les filets qui forment un réseau dont l'usage paraît être de lier les animaux du *Pyrosome* entre eux." In *n*, fig. 5, I imagine I recognize an ovisac. Lesueur describes it as one of the 'œufs' or fœtuses, which are well represented in figs. 8–11.

Contemporaneously with Lesueur,[1] that great, but unfortunate anatomist, Savigny, directed his attention to the *Pyrosomata,* the peculiarities of whose structure found, at length, an adequate expositor in him ; and his account of the anatomy of *Pyrosoma giganteum* is at once so lucid and so concise, that I cannot do better than reproduce it, as an introduction to my own memoir.

[1] The second memoir of the second part of the celebrated 'Mémoires sur les Animaux sans Vertèbres,' entitled "Observations sur les Alcyons à deux oscules apparens, sur les Botrylles, et sur les Pyrosomes," bears the inscription, "Lues à la première classe de l'Institut le 1er Mai 1815 ;" with the note, "Ce mémoire a été présenté le 17 Avril ; mais les travaux de la classe en ont fait différer la lecture."

The subjects of Savigny's observations were obtained at Nice by Risso, and by him sent to Cuvier.

"This *Pyrosoma* (*P. giganteum*) is a large cylindrical tube, composed of a gelatinous transparent substance, closed and rounded at one end, at the other, truncated and provided with an aperture narrowed by an annular diaphragm, which is not without analogy with the membranous circle of the *Botryllidæ*. The surface of the tube presents conical and smooth eminences of different sizes, some simple and very short, others longer and terminated by a lanceolate piece. Each eminence is pierced at its apex, behind the base of the lanceolate piece, when this exists, by a little circular hole, surrounded by a brown and projecting edge. This aperture, in my opinion, serves to give entrance to the water, and leads into the pharynx.

"The inner wall of the tube presents slight hemispherical enlargements, which correspond with the conical eminences of the external surface, and which are likewise pierced at their apices. The latter apertures, similar to the foregoing both in form and number, are situated opposite the anus, and give exit to the fæces.

"This diametrical opposition of the orifices of its cells is a novel peculiarity of the *Pyrosoma*, and determines the form of the whole body. The functions of each of these orifices seem to me to be sufficiently indicated by their relative position. One is naturally inclined to think that in this genus, as in the foregoing,[1] it is the most prominent orifice which transmits the food to the pharynx and which admits the water requisite for the branchiæ. Besides this, the water, incessantly renewed at the outer surface of the tube, could not be so rapidly or completely changed in its interior. The arrangement of the viscera in each animal agrees with this first indication.

"To describe the animals of the *Pyrosoma*, we may suppose the cylinder to be placed vertically on its base—I mean, on its rounded and closed end; for the opening of this body is evidently its summit. Each animal then represents an elliptical sac, compressed laterally, whose great axis is horizontal, and consequently perpendicular to that of the cylinder. This sac, formed by a delicate and transparent tunic, is attached to the cell which contains it, only by the circular opposed apertures of its two ends. The extremity which is turned towards the axis of the cylinder is simply rounded: that directed towards the circumference is prolonged into a neck, whose length is proportional to the projection which the cell makes externally, and whose orifice is provided with a festooned membrane. The lower edge of the sac exhibits the same brown and undulating vessels as the back of the

[1] [viz. *Botryllus.*]

foregoing species, and ought in consequence to be regarded as the corresponding region. The branchial cavity is very large; it occupies those two-thirds of the tunic which lie nearest the circumference of the cylinder: its bottom, which is completely open, communicates freely with the other third, which lodges the viscera of the abdomen. These are small, and situated on the right side. The space which they leave unoccupied is commonly filled by the fœtuses, which successively arrive and are developed there, as we shall see below. The structure of the branchial sac in the *Pyrosomata* may lead one to believe that the water absorbed by the oral, makes its way out by the anal orifice. This would be a feature of resemblance with the *Salpæ*, in which it is indubitable that the water takes this course. However this may be, the network which lines the cavity is otherwise organized: it is loose, and composed of fine, undulating, opaque white vessels, some of which are longitudinal, while others are transverse and cross the former at right angles—a character which is common to all the genera of this family. The network does not occupy the whole cavity, but only its two lateral walls; so that there are obviously, in this genus, two separate and opposite branchiæ, one on the right, and the other on the left, and which are much narrowed, and consequently distant, at the top. In the foregoing genera, the two branchiæ, although really distinct, are only separate behind. The pharynx is at the bottom of the branchial cavity, towards its upper angle. The œsophagus is curved sharply to be inserted into a notch of the stomach, which is placed behind the bottom of the branchial cavity. The stomach is fleshy, smooth, compressed, ovoid, or slightly cordiform. The intestine, very delicate at its commencement, suddenly enlarges; a short course brings it to the inferior edge of the tunic, where it receives the insertion[1] of a large organ analogous to the liver; afterwards it returns to the stomach, behind which it ends in a simple and rounded anus. The fæces are homogeneous, clear, yellow, and divided into little masses, the last of which is often already engaged in the atrial orifice (*oscule anal*), which seems to prove that the rectum has the power of elongating and of adapting itself to this orifice.

"I must remark, that the liver, or the organ which from its position may be regarded as such, is attached to the intestine by a bundle of divergent canals; that it is rounded, commonly opaque, rose-coloured, yellow or brown, strangulated above its insertion, and divided into from eight to twelve ribs, by grooves which converge from its base to its apex; it is very soft, and may be broken up into oblong pedunculated vesicles. I may add, as a remarkable fact, that, in

[1] An error: the organ in question being the testis.

many individuals, this organ is colourless, and that it resembles a cellular and transparent globule: it also varies greatly in volume; sometimes, and most frequently, it is of the size of the stomach, sometimes five or six times as large.[1]

"The nervous system of the *Pyrosomata* does not appear to differ essentially from that of the foregoing animals. There are, in like manner, two tubercles, one on each side of the neck of the branchial sac. The anterior or superior tubercle seems to give off several filaments, of which four ascend on this neck, while the others go to the opposite side. The posterior tubercle, which is here inferior, though very apparent in certain individuals, is imperceptible in most. There arise from it four opaque yellowish or brown vessels, which traverse the lower side of the tunic; they are evidently the four cords of the dorsal groove of the Ascidians.[2] Along the upper edge, opposite the four cords of the dorsal groove, are seen two wide, short canals, of a yellow or muddy-brown colour, placed parallel, and so closely united that they might be regarded as a single canal, bent like a siphon, and extending from the middle of the branchiæ to the œsophagus, where its two extremities end. The interior appears to be cellular.[3]

"This organ, which is sometimes empty and transparent, seems to me to be analogous to that which M. Cuvier regards as the ovary of the *Salpæ*, or at least as their oviduct; perhaps it is, at the same time, oviduct and fecundating organ.

"The ovaries[4] are orbicular or pyriform, symmetrically opposed to one another, and placed on the sides of the neck of the branchial opening, between the tunic and the branchial network, which they usually overlap. They communicate with two small, sometimes coloured ducts, which embrace the neck and descend as far as the loop formed by the siphon-like canals. These ovaries contain a multitude of rounded, very small, but very distinct ova.

"If I do not deceive myself, the manner in which these germs arrive at maturity is very curious. It would appear that while very small they become detached, one by one, from the ovary, and are

[1] Savigny has here clearly confounded the testis and the ovisac together under the one name of 'foie.' What he calls the ribbed organ is the testis; the cellular globule is an advanced ovisac.

[2] The 'anterior tubercle' is the nervous ganglion; the posterior merely the anterior end of the endostyle, which is described as the 'cords of the dorsal groove.'

[3] This 'organ' is the intestine of Lesueur, and, as I have said above, is nothing but a mass of blood-corpuscles accumulated in the hypopharyngeal sinus.

[4] These are not the ovaries, but probably, as I have already said, renal organs. What Savigny calls their ducts seem to be the lower parts of the peripharyngeal ridges.

successively lodged between the intestine and the bottom of the tunic; there they continue to grow and to be developed, until their final expulsion.

"In fact, we almost always find in this locality an isolated germ, which varies much in size. While small, it is only a perfectly white and transparent globule, in which a round aperture, like a mouth, is discernible; when somewhat larger, this hollow globule already exhibits four little reddish spots; and when larger still, these four spots have become a chain of four small but distinct little fœtuses, which encircle the globule for three-fourths of its circumference. Lastly, when it has acquired its full size, the four fœtuses, provided with all their organs, are united and form a complete ring. In this state it equals a third of the size of the individual which encloses it. It is, as one sees, a new *Pyrosoma* already composed of four animals, and will very soon be independent of the large *Pyrosoma* in which it has originated. How does it escape? I know not. If, as is probable, it makes its exit by the same aperture as the excrements, this opening must be capable of undergoing excessive dilatation.

"These observations, taken in conjunction with those which I have made upon *Botryllus*, demonstrate that the corpuscles contained in the ovaries of these animals are compound germs, not intended for the growth of systems, but for their multiplication. On the other hand, if we open a *Pyrosoma* or *Alcyonium*, we find, among the adult individuals, more or less developed embryos, which can only have proceeded from simple germs whose existence is manifested successively. These last, then, were all contained in the compound and primitive germ."

It is obvious from the last paragraph that Savigny was unaware of the origin of the latter 'embryos' by gemmation. In the 'Système des Ascidies' appended to the 'Mémoires,' Savigny forms the *Pyrosomata* into a family—the *Luciæ*, containing one genus, *Pyrosoma*, divided into two groups of species, *P. verticillatum* and *P. paniculatum*. In the former the animals are verticillate, or disposed in regular rings which project at intervals. It contains the single species *Pyrosoma elegans*, 15 lines long, with seven projecting rings, the first and the last terminal; the tuberosities composing the rings are lanceolate at the ends. There is no annular diaphragm around the wide mouth of the tube. It inhabits the Mediterranean, near Nice. Under the head of this species, Savigny makes the following important remark:—

"M. Lesueur has observed, that the whorl which terminates the tube at its small end is formed by four tubercles, *i.e.*, by four animals. He thinks that this disposition is peculiar to the species in question; but, with a little attention, the same arrangement is to be found in

the following species, where these four animals seem to be the representatives of the four little fœtuses which are developed in the egg before its extrusion."

The *Pyrosomata paniculata* are species in which the animals are not verticillate, and form very irregular circles, whose apices are everywhere irregularly projecting. This division comprises *P. giganteum* and *P. atlanticum*.

Pyrosoma giganteum has an almost cylindrical body, the external tuberosities being very unequal, hemispherical or conical; the most projecting having their appendage or terminal papilla lanceolate, subcarinate, and finely denticulated. The opening of the tube is commonly narrowed by an annular diaphragm. The total length of the largest tube is 14 inches; the opening, including the diaphragm, is 2 inches across; the individuals vary in size from 3–5 lines, according as the neck of the thorax is more or less prolonged—a circumstance which is independent of the age of the individual.

The *Pyrosomata* of this species presented several varieties:—

a. Body strongly stained with brown, as well internally as externally, apparently in consequence of a brown substance filling the branchial cavities. Terminal papillæ wide, and for the most part obtuse. Diaphragm very narrow, and leaving a large aperture. Total length 13–14 inches.

b. Body bluish or a little violet, perfectly transparent. Papillæ very narrow. No annular diaphragm at the aperture, which presented only very young individuals. Total length 6 inches.

c. Body bluish, perfectly transparent. Papillæ longer and more pointed than in the preceding varieties. An annular diaphragm, leaving but a very narrow aperture, around which almost all the animals were adult. Total length 5, 6, 7 inches.

This species inhabits the Mediterranean and Atlantic, bordering the French coasts.

In the description of *Pyrosoma giganteum*, Savigny gives some particulars not mentioned in his account quoted above. Thus, he says that the tunic offers but few vessels, "except upon the diaphragm which surrounds the aperture." The tunic is provided "below the abdomen with two transverse muscles, and, besides, is marked by interlacing muscular nervures, which are very fine, and hardly visible with a strong lens. . . . . The festooned membrane at the entrance of the branchial sac would be exactly circular if its posterior and inferior edge were not prolonged into a point.

"Branchiæ wholly separated behind, divided in front as far as their bases, rounded or acuminated at their apices; transverse vessels

18–25, increasing by degrees from the first, reckoning from the top, to the fifth or even the eighth; longitudinal vessels 11–17, the middle one only reaching the first transverse vessel, the following on each side attaining the second, and so on, the most external vessels being the shortest of all."

The other species, or the *Pyrosoma atlanticum*, has a conical body 6 or 7 inches long, with its external protuberances terminating in subulate points, and inhabits the equatorial seas.

Mr. F. D. Bennett exhibited some specimens of *Pyrosoma* at a meeting of the Zoological Society on the 25th of June, 1833, and gave an account of their phosphorescence. A paper by the same author, "On marine *Noctilucæ*," printed in the 'Proceedings' of the Zoological Society for 1837, contains further remarks on the same subject, and the statement that the 'sphincter-like' membrane which surrounds the cloacal aperture is capable of contraction.

In the 'Comptes Rendus' for 1840 (tom. x. p. 285), M. Milne-Edwards published some important observations on the circulation of the *Pyrosomata*, by which he not only demonstrated, for the first time, the existence of a heart, but proved that in these, as in most other Ascidians, this organ is subject to a regular reversal of its peristaltic contractions. The regular movement of the branchial cilia is also noted in this communication. With the exception of this valuable contribution to our knowledge of the genus, I am not aware that, with the exception of M. Vogt's short paper, to be noticed below, any account of observations on *Pyrosoma* has been published since Savigny's time, except my own memoir "On the Anatomy and Physiology of *Salpa* and *Pyrosoma*, together with remarks on *Doliolum* and *Appendicularia*," contained in the 'Philosophical Transactions' for 1851.

In this memoir I have detailed the results of investigations, made under difficult circumstances and with but a few hours at my disposal, upon a single specimen of what I suppose to have been *Pyrosoma atlanticum*.

By the publication of this essay there was added to what had been already made known, an account of the tubules which envelope the intestine, and open into the stomach by a common axis. The lateral circular palettes, called 'ovaria' by Savigny, were shown not to have the function assigned to them. The blood was stated to be contained in one great sinus which extends through the whole of the body; and the reversal of the motion of the heart, observed by Milne-Edwards, was confirmed. The 'four undulating vessels' of Savigny were shown to be the expression of an endostyle, such as exists in other

Ascidians. It was further stated that the edges of the vertical branchial bars, only, were ciliated. The ciliated fossa, the peripharyngeal ridges, the languets, and the otoliths were described. The 'liver' of Savigny was shown to be the testis; and the form and mode of development of the spermatozoa were described. The characters of the female organs were determined; the presence of spermatozoa in the duct of the ovisac was observed; and it was proved that the so-called 'simple embryos' of Savigny are formed by gemmation. None of the compound embryos were observed in this specimen, however; and hence I have always felt a great desire to re-examine *Pyrosoma*, for the purpose of ascertaining the real nature and origin of such singular bodies. From Savigny's habitual accuracy, I had no doubt of their existence and essential correspondence with his account; but it seemed impossible that they should be developed in the way he describes.

In his valuable memoir "Sur les Tuniciers nageants de la mer de Nice[1]," M. Vogt confirms my account of the structure of *Pyrosoma*, and adds some remarks, which are, unfortunately, very brief, upon the fœtuses discovered by Savigny, and which I failed to find in my specimen. In pl. 10. figs. 9 & 10, some sketches made in 1847, and referred to in a passage of the 'Ocean und Mittelmeer' of the same author, published in 1848, are given. They are thus described at p. 89 of the present essay:—

"In fig. 9 the ovisac is seen below the testicle, immediately in front of the posterior aperture of the body. It has a rounded form, and contains an enormous, yellowish-coloured and almost transparent ovum, below which again are accumulated oviform masses which exhibit a granular vitellus. I could see no further structure in these ova; but, I must confess, I did not carry my investigations very far. In fig. 10 I have given an outline-sketch of the individual which exhibited five young in its ovisac. The latter has a rounded form, but is much larger than in the foregoing specimen, and having pushed the viscera downwards, it has extended towards the branchial cavity, in which it forms a kind of hernia."

Fig. 9 represents, in fact, an ovisac with a segmented blastoderm, while in fig. 10 the 'five young' are the cyathozooid and the four ascidiozooids of a young fœtus.

I do not understand how the ovisac in M. Vogt's specimen can have occupied the position in which it is figured in fig. 10, the more

[1] "Recherches sur les Animaux inférieurs de la Méditerranée," Mém. de l'Institut National Génevois, tom. ii., 1854.

especially as in fig. 9 it lies in the same place as that in which I have always found it, viz. in the large mid-atrium and altogether behind the intestine. M. Vogt concludes by putting forward the hypothesis that the ova pass down the canal of the ovisac into the neighbourhood of the intestine, where an incubatory cavity, in which their final development takes place, is formed for them in the thickness of the inner tunic.

"This incubation, perhaps, takes place only during certain periods of the year, or of the life of the zooid, whence the incubatory cavity is found only in some individuals and not in all. The formation of ova in the projecting ovary would continue for a certain time. The ova would pass, as they became fecundated, into this incubatory cavity, would develope there, and would ultimately be set free to lead an independent existence. Perhaps, indeed, the incubatory sac may be thrown off bodily, and thus give rise to the base of the new cylinder." (*l. c.* p. 90.)

These observations and suggestions obviously leave much room for further inquiry, and my satisfaction will be easily understood when that opportunity of renewing my investigations which I desired, but little expected, was unexpectedly afforded me. In October of the year 1859, Rear-Admiral FitzRoy, F.R.S., the indefatigable Superintendent of the Marine Department of the Board of Trade, kindly forwarded to me a very beautiful specimen of *Pyrosoma giganteum*, taken by Captain Callow[1] in the North Atlantic, about 400 miles S. of the Cape De Verd Islands, in the month of August of that year, and admirably preserved by immersion in strong spirits. I was aware, from former experience, that the textures of Ascidians, in general, are admirably conserved in spirit-specimens which are even many years old; and I therefore commenced my inquiries with a sanguine expectation of being able to make out something about the origin of the compound embryos, which a cursory inspection of the specimen proved to exist in abundance. I must confess, however, that I had no anticipation that researches conducted upon a preserved specimen of any animal could be followed out so far as I have been led, step by step, to carry these. And had I not had the opportunity of showing many of my preparations to observers of experience and authority, who can bear witness, at any rate, to the perfect distinctness of the most important of the appearances described, I should hardly have hoped to secure a patient reception for delicate embryo-

[1] Finding a specimen could be procured in no other way, this gallant and skilful seaman swam for that he obtained. He informs me that it emitted a strong bluish-white light, sufficient to read small print by.

logical inquiries which profess to have been conducted upon thin sections of a spirit-specimen, rendered clear by glycerine.

I have already published a brief notice of the most important facts which have been developed by my investigations in a paper published in the 'Annals of Natural History' for January 1860, and in a communication to Section D. of the Meeting of the British Association at Oxford in July 1860.

§ 2. *The Anatomy of* PYROSOMA GIGANTEUM.

In the specimen of *Pyrosoma* under description, the ascidiarium[1] is a firm, hollow, conical body, 4 inches long, and about $\frac{7}{8}$ths of an inch wide at its broad, open end, whilst its rounded apex measures hardly more than half an inch. The translucent, colourless wall of the ascidiarium is on an average about $\frac{3}{16}$ths of an inch thick; but it thins towards the open end, ending in a sharp ledge or rim, which is bent horizontally inwards and ends in a sort of circular valve-like lip, nearly $\frac{1}{5}$th of an inch wide, around the aperture of the central hollow or cloaca.

In relation to the ascidiozooids, the closed, apical, end of the ascidiarium is dorsal or hæmal, inasmuch as the heart is situated on that side of the body of every ascidiozooid which is turned towards the apex. The nervous ganglion, on the other hand, is on the opposite side of the body, so that the open extremity of the ascidiarium is its neural end.

The outer surface of the ascidiarium is rendered uneven by conical eminences, which are scattered over it at irregular intervals, and which are elongated on their neural sides into longer or shorter processes. Among these lie similar eminences without such processes and varying in elevation, until they hardly project at all above the general level of the convex surface of the ascidiarium. Each of these eminences bears a small rounded aperture, the oral opening of an ascidiozooid; and there are other, similar, apertures, dispersed between the eminences. In the specimen under description, the ascidiozooids are almost colourless, or have at most a very pale brownish hue; but how much of this colourlessness may be due to the action of the spirit, I do not know.

Such is the general appearance of the ascidiarium. To examine its internal structure, it is expedient to make sections with a razor in

[1] The entire body of a compound Ascidian may be conveniently termed the *ascidiarium*, while the separate zooids may be called *ascidiozooids*.

various directions. Although not absolutely necessary, I found it extremely advantageous to treat these sections with glycerine, or with a mixture of gum and glycerine—a process which not only has the advantage of rendering the tissues extremely transparent, but of preserving the preparations for a very long time unchanged.[1] It might have been reasonably expected that the tissues would undergo serious distortion in such a medium, but this is not the case; on the contrary, the most delicate structures, such, for instance, as the cilia upon the branchial sac, are most exquisitely exhibited in glycerine preparations. As I have said above, I have often had occasion to remark the perfection with which the tissues of the Ascidians generally are preserved by strong spirit, and the subsequent addition of glycerine seems only to increase the transparency of such preserved specimens, without otherwise altering them.

When a segment is cut out of the ascidiarium of *Pyrosoma* and examined from the inner or cloacal side, the surface presented to the eye is seen to be tolerably smooth, or at most minutely mammillated, and to present numerous small apertures, each of which corresponds with, and is opposite to, one of the apertures upon the outer surface: while the latter, in fact, is the oral, the former is the atrial[2] orifice of one of the ascidiozooids. In a thin vertical and radial section (Pl. XXX. [Plate 29] figs. 1 & 4), the orifices are seen to be connected together by a comparatively wide, somewhat oval cavity, composed of the branchial chamber and the atrium of the ascidiozooid, which are separated from one another only by the perforated branchial sac, stretched like a bag-net from one wall of the cavity to the other. It would be a difficult operation to perform, but a fine hair *might* be passed in at the oral and out at the atrial aperture, through one of the meshes of the branchial sac, without injuring any organ.

[1] Some which have now been more than a year in my possession exhibit no alteration.

[2] M. Milne-Edwards, in his "Observations sur les Ascidies Composées," 1839, describes the cavity which surrounds the branchial sac, and into which the branchial currents flow, as the 'chambre thoracique;' that part of it which receives the fæces and generative elements he terms the 'cloaca,' while he retains the name of 'anus' for the external aperture of this cloaca. From experience of the inconvenience of this phraseology, I was led some years ago ("Researches into the Structure of the Ascidians," Reports of the British Association, 1852), to propose the term *atrium* to indicate the 'thoracic chamber,' and to reserve the term *cloaca* for the chamber common to several or many ascidiozooids, as in *Botryllus*, &c. The aperture of the atrium may be termed the *atrial aperture*. The membrane which lines it, and which was in part distinguished by Milne-Edwards in the memoir cited, is the *atrial tunic*. The cellulose integument of an Ascidian is for me the *test*. The body-wall which underlies and gives origin to this test, I term the *external tunic*. The proper wall of the alimentary canal (with Milne-Edwards, I regard the branchial sac as a dilated pharynx) is the *internal tunic* of the body. For the meaning of any other terms not explained in the text, I must refer to my "Memoir on *Salpa* and *Pyrosoma*" already cited.

From what has been said, it follows that each fully-formed ascidiozooid must be equal in length to the thickness of that part of the wall of the ascidiarium in which it occurs; and the whole ascidiarium may be regarded as a succession of tiers of ascidiozooids enveloped in a common test.

The extreme apex of the cone (Pl. XXX. [Plate 29] fig. 5) is formed by only four ascidiozooids ranged round a common point. In the next tier there are at least twelve, and the number increases until, in the widest part of the ascidiarium, there are between thirty and forty in a tier. It should be understood, however, that there is nothing very regular in the arrangement of these tiers, and that the zooids in any given tier are of very various sizes and degrees of development.

The Ascidiarium presents for study (1) the ascidiozooids, and (2) the common test which envelopes them[1].

The Ascidiozooids.—In investigating the structure of the ascidiozooids, an example from the middle region of the ascidiarium may most conveniently be selected for study. Such an ascidiozooid is represented in longitudinal section in Pl. XXX. [Plate 29] fig. 1, in transverse section in fig. 2, and from above and partly in section in fig. 3.

It is somewhat irregularly fusiform, a good deal longer than deep, and deeper than broad. Its outer extremity exhibits the oral aperture, which lies upon the hæmal side of one of the above-mentioned conical protuberances, and is overhung by a tongue-like process of the test—the *labial process*, by whose outgrowth, indeed, its relations and appearance have become so completely altered, that it will be better to become acquainted with the character of the oral aperture in a less modified specimen. On examining one of those oral apertures, in fact, which are hardly, or not at all, raised above the general level of the outer face of the ascidiarium, the plane of the oral aperture is seen to be perpendicular to the axis of the body (taking a line drawn from the oral to the cloacal aperture as that axis). A circular sphincter, composed of a band of unstriped muscular fibres, surrounds the oral entrance, being attached where the lining membrane of the alimentary tract (inner tunic: see note, p. 325) and the integument (outer tunic) pass into one another. The inner diameter of the circular sphincter is $\frac{1}{150}$th of an inch; but the diameter of the oral passage itself is far less, amounting to not more than

[1] In the present memoir I propose to confine myself as nearly as may be practicable to anatomical and embryological details, reserving the many interesting histological peculiarities of *Pyrosoma* for a future occasion.

$\frac{1}{1000}$th of an inch. This results from the circumstance that the test is thickened at the margins of the mouth, so as to diminish its aperture to this extent; and it is at the same time puckered, so that when viewed from without, a number of fine grooves appear to radiate from the lips of the aperture. These must not be confounded with certain fine fibres which radiate from the outer margin of the sphincter into the test, and are perhaps muscular (Pl. XXX. [Plate 29] fig. 6).

The test ceases to be traceable upon the walls of the oral cavity a little within the sphincter; and where it ends, the inner tunic is produced inwards into a broad fold with lobed edges, which takes the place of that circlet of tentacles which is found in this position in most other Ascidians. I shall therefore term this the *tentacular fringe*. It is divided altogether into thirteen lobes, of which twelve, though irregular, are tolerably similar and roughly symmetrical, while the thirteenth is situated in the middle of the hæmal half of the circlet, and is very different in form and size from the rest. It is, in fact, three or four times as long as they are, and is divisible into a broad trilobed base, shaped somewhat like an ace of clubs, and a narrow fringe-like terminal portion. This may be distinguished by the title of the *hæmal tentacle* (Pl. XXX. [Plate 29] figs. 6, *6a*).

The form, size, and relative position of the oral aperture remain the same in ascidiozooids which have the oral aperture mounted upon a very short cone; but as the cone enlarges, its hæmal grows faster than its neural side, and finally becomes prolonged into the labial process, which bends over at a right angle to the direction of the axis of the zooid.[1] Concomitantly with, and apparently as a result of, this development of the labial process, the plane of the oral aperture gradually shifts, until, in the first place, it lies parallel with the axis of the zooid, and then continuing to turn, as it were, on its hæmal margin, it eventually takes up a position perpendicular to the axis of the ascidiozooid again, but exactly the reverse of that which it had at first. The labial process so completely overhangs the oral aperture when this stage is attained, that the free access of the water to the interior of the zooid must, one would think, be somewhat impeded.

Two very delicate muscular bands, attached to the inner tunic, succeed one another at short intervals behind the aperture of the mouth, within which the buccal cavity rapidly widens, until it attains

[1] In the figures given by Lesueur and by Savigny, the axis of the labial process is parallel with that of the body. In most of the ascidiozooids of my specimen, the end of the process is turned towards the hæmal side, but in some it is bent the other way.

its maximum at about the end of the first fourth of the whole length of the zooid. At this point the buccal cavity ends and the pharyngeal or branchial sac commences, the boundary-line between the two being marked by the anterior end of the endostyle and of the epipharyngeal folds, in the middle line of the hæmal side; the peripharyngeal ridge at the sides, and the ciliated sac on the neural side. On each side, opposite the middle of the peripharyngeal ridge, is the circular patch-like yellowish organ regarded as the ovary by Savigny.

The *peripharyngeal ridge* (ciliated band, *mihi*, Mem. on *Salpa*) is a structure which I have found in all the ordinary Ascidians which I have examined. In *Pyrosoma* it is a sort of ridge or inward process of the inner tunic, less than $\frac{1}{900}$th of an inch broad, on which the epithelial lining of the tunic is peculiarly modified, so as to present the appearance of a multitude of transverse rows of elongated corpuscles, each row being set obliquely to the long axis of the band, so as to be inclined from the hæmal side and behind, forwards and to the neural side. These corpuscles are provided with short and delicate cilia. If the peripharyngeal ridge is traced upwards on the inner tunic, it is found to reach the anterior extremity of the cleft-like entrance to the endostyle, and there to pass into a narrow series of similar corpuscles which runs parallel with, and indeed may be said to form the outer part of, the projecting lip or *epipharyngeal fold* ('dorsal folds' of Savigny and others) which bounds the entrance to the endostyle laterally. Arrived at the posterior extremity of the epipharyngeal fold, these prolongations of the peripharyngeal ridge, or, as they may be termed, epipharyngeal ridges, unite with one another and pass down as a single *posterior epipharyngeal ridge* along the middle line of the posterior wall of the pharynx to the œsophageal aperture, before reaching which the single ridge divides, and its branches soon cease to be further distinguishable. On the neural side, the two peripharyngeal ridges pass on to the elevation of the inner tunic in which the ciliated sac opens, and unite upon its posterior half, widening as they do so, whence their junction forms a triangular area with its apex directed backwards.

The very singular structure which I formerly termed the *endostyle*, and which I was at one time inclined to regard as a kind of internal shell, is, in reality, a longitudinal fold or diverticulum of the middle of the hæmal wall of the pharynx, which projects as a vertical ridge into the hæmal sinus, but remains in free communication with the pharynx by a cleft upon its neural side. In consequence of the thickness and opacity of the epithelium which lines the fundus of this

fold, it appears (especially in the fresh state) like a strong hollow rod mounted upon a thin ridge-like plate.

Transverse sections, however, demonstrate the true nature of this structure with perfect clearness (Pl. XXX. [Plate 29] fig. 8). The bottom of the diverticulum is seen to be occupied by two stout cords, formed of elongated epithelium-cells set perpendicularly to the axis of the cord. These cords are separated from one another by a slight interval. Externally and below they are in contact with two lateral cords of similar cells. Anteriorly the lateral pass into the middle cords, while the latter project beyond the anterior boundary of the groove-like entrance into the cavity of the endostyle (and, consequently, of the anterior ends of the lips or epipharyngeal folds which bound it) and, coated by a process of the inner tunic, constitute the free, rounded, anterior termination of the endostyle.

Posteriorly, the same confluence of the median and lateral cords takes place; but here the endostyle extends much further beyond the limit of the groove and its bounding folds, and constitutes a free, hollow cylindroid or conical process, which, as we shall see, plays a very important part in the process of gemmation, where I shall have occasion to speak of it as the *endostylic cone.*

The *hypopharyngeal band* is not, as in many Ascidians, separated for the greater part of its length from the neural wall of the ascidiozooid. On the contrary, in consequence of the position of the œsophageal aperture close to the neural wall of the branchial cavity, and the non-extension of the atrium forwards in the middle line, the hypopharyngeal band is represented only by the inner tunic of this neural wall, which lies parallel with the outer tunic, and is separated from it only by the neural sinus, which usually contains a great aggregation of blood-corpuscles. These corpuscles are commonly aggregated more densely in the posterior two-thirds of the hypopharyngeal sinus, and not unfrequently are divided, more or less completely, into two lateral portions by a median clear space. When this state of things exists, the hypopharyngeal sinus, under a low power, presents exactly that appearance which is figured by Savigny as a siphon-like tube.

The inner tunic of the hypopharyngeal band is produced in the middle line into eight slender conical processes—the *languets*, which are situated at tolerably equal distances from one another. Thus both the neural and the hæmal walls of the pharynx are separated from the outer tunic in the middle line by nothing but the corresponding sinuses; and the same holds good of the lateral wall in the region of the peripharyngeal ridge. But at any point behind this, either a vertical and transverse section, or a view from above, shows that the inner

tunic (or pharyngeal wall) is separated from the outer tunic by a more or less wide space, enclosed within a membrane which is totally distinct from both the outer and the inner tunics, except at the atrial orifice, where it passes into the former, and at the anus, where it becomes continuous with the latter.

Except for these two breaks, the membrane in question (which is the third tunic of Milne-Edwards, and is what I have elsewhere termed the *atrial tunic*) might be compared to a closed serous sac, reflected over the viscera, on the one hand, and over a part of the external tunic, on the other, but leaving a space between itself and both these parts, which space is filled with blood, and forms a part of the general system of sinuses of the body. A careful examination of the side view (Pl. XXX. [Plate 29] fig. 1), the upper view (fig. 3), and the transverse section (fig. 2) will render this statement intelligible.

In the first, the atrial tunic is seen to be reflected over the posterior face of the stomach and first part of the intestine, and then to form the roof and the floor of the cavity, which lies between the intestine and the atrial aperture, and which I shall term the *mid-atrium*. In fig. 3, the atrial tunic is shown to be continued forwards at the sides of the intestinal canal on to the pharynx, united with which, it forms the branchial sac. Arrived close behind the peri-pharyngeal ridge, it is reflected on to the external tunic, and then passes directly backwards to the atrial aperture. The testis and ovisac, which are seen, in this view, over the alimentary canal, lie altogether above the roof of the mid-atrium (fig. 1), and therefore do not in any way interfere with the free and wide communication of the mid-atrium with the two spaces, or *lateral atria*, which lie between the branchial sac and the body-wall, and are well shown in the transverse and vertical section (fig. 2). Both in this section and in fig. 3, short cords are seen to pass between the parietal and the visceral layers of the lateral atria. They are hollow, and place the parietal sinuses in communication with those of the branchial sac.

It follows from what has been said that the wall of the *branchial sac* of *Pyrosoma* (and, I may add, of all Ascidians with a similar respiratory apparatus) consists, internally, of that portion of the alimentary tract which lies in front of the œsophagus and behind the mouth (or, in other words, of the pharynx), and, externally, of the visceral layer of the atrial tunic. Now, these two membranes do not remain entirely separated by the interposed sinus, but are united at regular intervals, so as to give rise to hollow *vertical bars* separated by equally long vertical clefts—the *branchial stigmata*.

Of these stigmata there are about thirty on each side. The most anterior and the most posterior ones are shorter than the others. Anteriorly, in fact, the first is not more than one-third or one-fourth, or even less, as long as the vertical height of the branchial sac. The stigmata, however, increase in length up to the sixth, and then acquire nearly the height of the sac, so as to leave only a small imperforate space on each side of the languets, on the neural side, and of the endostyle, on the hæmal side. Posteriorly the last four or five also gradually diminish, until the hindmost of all is not larger than the foremost.

The vertical bars bounding the stigmata are fringed by a single series of elongated corpuscles, each of which bears a row of long cilia, and (in the dead state, at any rate) all these cilia project outwards into the lateral atria[1].

The branchial stigmata just described are subdivided into quadrate meshes by some fifteen *longitudinal bars* which lie altogether on the inner side of the vertical ones, to which they are attached by their outer edges, projecting like so many narrow shelves into the pharyngeal cavity, and, as I observed in my earlier memoir on this animal [2], are devoid of cilia. They terminate abruptly at their anterior and posterior ends, and they do not exhibit the small denticulations along their free edges which I have described in *P. atlanticum*. The water taken in by the oral aperture must pass with perfect ease through these meshes, and then, impelled by the cilia on the vertical branchial bars, make its way through the lateral atria and, on each side of the intestine, to the mid-atrium, whence it finds an exit by the atrial aperture.

As to the proper *digestive canal*, the wide aperture of the œsophagus lies at the posterior, neural, angle of the pharyngo-branchial sac, and has an irregular figure; but whether this irregularity is normal, or arises from the collapse of its walls after death, I cannot say. The œsophagus narrows as it passes back, and then curves sharply round towards the hæmal side, to open, after a very short course, into the large oval stomach, which lies immediately behind the middle of the branchial sac, invested, everywhere but in front, by the atrial tunic, and bathed in the blood which lies between it and that tunic. At its pyloric end it gives rise to the narrow commencement of the intestine, which, after suddenly dilating and turning forwards and to the hæmal side, bends back sharply upon itself,

[1] In the living condition, as Milne-Edwards has hinted, and as I have shown in my memoir (*l. c.* p. 583), the cilia upon opposite sides of a branchial stigma move in opposite dire tions.

[2] *Loc. cit.* pl. 17, fig. 3, and p. 583, line 4, where the word 'sinus' should be 'ones.'

and passing backwards to the neural side and to the right, ends opposite the middle of the stomach in the abruptly truncated anus, which opens into the atrium.

In my memoirs on *Salpa*, *Pyrosoma*, and *Doliolum*, already referred to, I have described, in all these genera, a remarkable system of fine transparent tubes which ramify over the intestine, and eventually open by a single duct into the stomach. I have asked (*l. c.* p. 570), does this *tubular system* represent a hepatic organ? or is it not more probably a sort of rudimentary lacteal system—a means of straining off the nutritive juices from the stomach into the blood by which these tubes are bathed? In *Pyrosoma giganteum* the duct of the system is very obvious, opening into the stomach in front of the origin of the intestine, and somewhat enlarged at its opposite end.

Krohn has described the structure and development of a similar system of tubuli in *Phallusia*,[1] and I have since [2] found an organ of the same nature in *Phallusia*, *Cynthia*, *Molgula*, *Perophora*, *Botryllus*, *Botrylloides*, *Clavelina*, *Aplidium*, *Didemnum*, and, indeed, in all genera of Ascidians which have come under my notice, except *Appendicularia*. In some species of *Didemnum*, I have observed that the duct dilates almost at once into a large spheroidal sac. I suspect that Savigny was the original discoverer of this system (see his memoir on *Diazona*, *l. c.* p. 176, and the description of pl. 12). The existence of these tubuli in *Salpa*, *Doliolum*, and *Pyrosoma* has been confirmed by all subsequent observers. M. Vogt, however (*l. c.* p. 31), affirms that the organ consists of solid branches, and that it partakes of the nature of a muscular organ, in neither of which opinions can I possibly concur. I have no doubt whatever that the apparatus is a glandular organ, and that it performs a part, at any rate, of the functions of a liver.

The *vascular system* of *Pyrosoma* is exceedingly simple; nor could we anywhere find a more convincing example of the validity (in some cases, at any rate) of Milne-Edwards's views of the circulation in the Mollusca than is offered by this animal. The heart lies close to, and apparently connected with, the right side of the posterior and hæmal wall of the pharynx, between the endostyle and the bend of the intestine; and it appears to have exactly the same structure as in *P. atlanticum*. There are no vessels, the whole interspace between the inner tunic and the outer, or between these and the atrial tunic, being one vast blood-sinus, with which the canals in the branchial bars communicate at each end. I have spoken of the

[1] "Ueber die Entwickelung der Ascidien," Müller's Archiv, 1852, p. 331.

[2] See Reports of the British Association, 1852.

hæmal and of the hypopharyngeal sinuses merely as a matter of convenience; in point of fact, the general blood-cavity is not naturally divided into distinct sinuses[1].

The *nervous system* consists, as in *Pyrosoma atlanticum*, of a single ganglion, of an oval shape when viewed sideways, but somewhat heart-shaped when seen from above, its narrower end being turned backwards. It is about $\frac{1}{120}$th of an inch long, and is composed of a dark granular mass invested by a delicate structureless membrane. It lies between the inner and outer tunics, the former being raised, so as to form a slight protuberance over it. On the posterior half of this protuberance lies the broad lower median portion of the peripharyngeal ridge. In its anterior half, the opening of the ciliated sac appears. The principal nerves given off from the ganglion are the following. Two, a smaller internal and a larger external, pass from the antero-lateral parts of the ganglion, forwards towards the oral aperture, branching as they go. I suspect that a nerve runs up on each side, beneath the peripharyngeal ridge; but I cannot make sure of the fact. A considerable nervous trunk is given off to the postero-lateral walls of the body; and, finally, two delicate trunks arise posteriorly, one on each side of the middle line, which run back, so as to have the languets between them, and passing up at the sides of the œsophageal aperture, are lost under the divisions of the posterior epipharyngeal ridge.

In *Pyrosoma atlanticum* I observed a mass of deep-red otoliths in contact with the posterior end of the ganglion (*l. c.* p. 583), but no

[1] I have described the circulatory system of *Salpa* in similar terms to these, in my memoir on *Salpa* and *Pyrosoma*, and notwithstanding the criticism my statements have received both from M. Vogt and Prof. Leuckart, I must maintain their correctness. M. Vogt affirms that I have committed 'a grave error' in declaring the blood-canals of *Salpa* to be lacunæ between the two layers of the mantle,—apparently supposing that I mean thereby the test and the external tunic, and forgetting my careful discrimination of test, outer tunic and inner tunic, at p. 585 of the memoir cited. In fact, nothing can be easier than to observe the entire distinctness of the inner and outer tunics in a bud or embryo of *Salpa* or *Pyrosoma*—to see that the viscera and blood-canals do really lie between these tunics, and that they are by no means, as M. Vogt states, lodged in cavities excavated in the 'inner mantle.' Prof. Leuckart has equally mistaken my meaning when (*l. c.* p. 14) he ascribes to me a participation in Eschricht's opinion as to the existence of a serous sac surrounding the body of *Salpa*. My words in the passage cited by Prof. Leuckart are, "In very young *Salpæ*, this space [the interval between the inner and outer tunics] is like the cavity of a serous sac." Still less can I find in my memoir any such opinions as those ascribed to me in the note to p. 43 of Prof. Leuckart's valuable memoir. While on the subject of errors, however, I am glad to take the opportunity of pointing out that several statements made at second-hand in my memoir, regarding Ascidians other than those specially described, are incorrect. The diagram of *Pelonaia* (pl. 19), again, is altogether erroneous—this Ascidian differing, as I have since found, in no essential respect from *Cynthia*.

such structures are discernible in the present species. The *ciliated sac* ('tubercule antérieur' of Savigny)—an organ of universal occurrence among Ascidians—is in *Pyrosoma giganteum* an elongated, laterally compressed, funnel-shaped bag, about $\frac{1}{100}$th of an inch long, which lies in the sinus, and, passing obliquely forwards and towards the hæmal side, opens as above described. Its aperture has somewhat prominent lips, and is rather narrower than its upper portion. The posterior end of the sac appears to terminate cæcally, and is applied against the posterior surface of the ganglion. The middle of the hæmal side of the sac sometimes appears to be connected with a spheroidal tubercle, whose axis forms nearly a right angle with that of the sac.

The muscular system is exceedingly simple in this species of *Pyrosoma*, consisting, besides the oral sphincter and buccal muscles already mentioned, of only an atrial sphincter and the 'mid-atrial' muscles.

The atrial aperture (fig. 7) is even smaller than the oral, not measuring more than from $\frac{1}{800}$th to $\frac{1}{500}$th of an inch in diameter. Radiating striæ diverge from its margin on the surface of the test, which, as at the oral aperture, forms a thick lip, and is continued for some little distance inwards upon the wall of the mid-atrium. A sphincter formed of pale smooth fibres, and constituting a circular band $\frac{1}{168}$th of an inch in diameter, is developed at the junction of the external and atrial tunics. There is a similar but less distinct appearance of radiating fibres to that exhibited at the oral sphincter.

The mid-atrial muscles (g_2) are broad flat bands of smooth muscular fibres, which lie in close contact with, and apparently attached to, the atrial tunic. One of these bands occupies about the middle two-fourths of the height of each lateral wall of the mid-atrium, and has a direction perpendicular to the axis of the ascidiozooid. The bundle of fibres spreads out a little at each end, and then seems to be inserted by a sort of tendon into the outer tunic. Close to this tendinous insertion, at either end, a bundle of fibres (whether merely fibrous or muscular I cannot say) arises, and passes, partly to the nearest similar insertion of one of the mid-atrial muscles of the ascidiozooid above or below, partly to the same point of the mid-atrial muscle of some other ascidiozooid. Hence, when the wall of the ascidiarium is viewed from within, it presents such an interlacement of fibres as that exhibited in fig. 9.

These muscles, in contracting, must tend to diminish the capacity of the atrium of the ascidiozooid to which they belong, and, if they all

act together, to shorten and narrow the ascidiarium. I do not suppose that their effect in the latter direction can be very great; but it might well be sufficient to account for the slight contraction of the whole ascidiarium, and consequent retrogressive motion, observed by Péron and others.

In my previous memoir, I have pointed out that the round, granular, yellowish patches on each side of the entrance of the branchial sac, and opposite the middle of the peripharyngeal ridge, are not, as Savigny imagined, the ovaries. I am greatly inclined to regard them as renal organs, but for the present defer the discussion of their structure and functions.

The reproductive organs of each ascidiozooid of *Pyrosoma* may be divided into actual and potential—the *genitalia* of the ascidiozooid itself, and the blastema whence the genitalia of its buds will take their origin. I shall call this last the generative blastema; while the genitalia proper are divisible, as I have already pointed out, into a single ovisac and a single testis. Both ovisac and testis are situated in the left five-sixths of the roof of the mid-atrium; but the testis is to the right, the ovisac to the left. The size of both these organs has a definite relation to the age and advancement in development of the ascidiozooid in which they occur, being larger and more advanced as it is older and nearer perfection. Hence the early stages of both ovisac and testis can only be observed in buds and young ascidiozooids. The generative blastema will be most conveniently considered in connexion with the process of gemmation and in describing the most advanced condition of the fœtus. The description of the ovisac will form the most fitting commencement of the history of sexual propagation in *Pyrosoma* (§ 3); all that remains, therefore, is to give in this place some account of the structure of the testis and of the character of its products.

The testis lies in the hæmal sinus above the mid-atrium, and on the right side of the ovisac. It consists of about a dozen cylindroidal cæca, free at their neural ends, but connected at their hæmal extremity with the dilated upper end of a vas deferens, which passes directly to the neural side and somewhat backwards, to open by a slightly raised papilla on the roof of the mid-atrium. The cæca are $\frac{1}{50}$th of an inch long, or thereabouts. Each consists of a delicate structureless membrana propria investing an aggregation of spheroidal corpuscles about $\frac{1}{4000}$th of an inch in diameter. Near the attached end of each cæcum the rod-like heads of the spermatozoa become visible, and gradually take the place of the spheroidal cells. The duct has the same structure as the cæca. It presents an upper and

a middle dilatation, but is not more than $\frac{1}{700}$th of an inch wide at its termination. The middle dilatation is usually full of closely packed spermatozoa.

The structure which has been described is characteristic of any of the fully-formed ascidiozooids in the middle of the ascidiarium, or towards its apical end, in which regions the number of such ascidiozooids bears a large ratio to the total.

But towards the open end of the ascidiarium fully-formed ascidiozooids become scarcer and scarcer, until, close to the inflected cloacal lip, none are discernible. On the other hand, all those ascidiozooids which are to be found in this region possess an appendage which is not to be discovered in the others, in the shape of a long tubular diverticulum of the external tunic, or stolon, which extends from the neural side of the body, behind the œsophageal aperture, into the lip of the cloaca, at whose free edge it ends in a cæcum. The walls of these diverticula, composed of the external tunic only, exhibit strongly marked parallel longitudinal striæ, as if they were composed of muscular fibrillæ.[1]

The test.—The common integument, or test, in which all the ascidiozooids are enclosed, appears to the naked eye to be quite glassy and homogeneous; but when thin sections taken in various directions are submitted to the microscope, it is found to possess marked structural peculiarities. Dispersed through its general substance are numerous cells with radiating processes, like connective-tissue corpuscles, and containing a central endoplast or nucleus. The cells measure on an average $\frac{1}{4000}$th of an inch in diameter; and their processes become very fine before they are lost in the surrounding nearly homogeneous matrix. In two regions this general structure is departed from. At the cloacal wall of the test, there lies immediately beneath the surface a thin film of reticulated tissue, consisting of cells similar in their essential structure to those just described, but set more closely, more granular, elongated, and united together by the coalescence of their processes. Again, in a plane which would correspond with the peripharyngeal ridges of the ascidiozooids, and therefore near the outer surface, the test exhibits a very faint longitudinal striation, as if it were fibrillated.

[1] Savigny has figured these stolon-like diverticula in his pl. 22. fig. l, 1, and he speaks of them in the "Système des Ascidies," p. 208, where in characterizing the test of *Pyrosoma giganteum*, he says that it generally presents few vessels, "except in the diaphragm of the opening." He appears not to have been acquainted with the origin of these "vessels." In describing his variety *c* of this species, he states (*supra*) that the opening was surrounded by animals which were almost all adult.

There is no distinct epidermic layer on either face of the test. The corpuscles are, as usual, stained dark yellowish brown by iodine ; while the matrix yields, though weakly, the characteristic reaction of cellulose.

§ 3. *The Agamogenesis by Gemmation of* PYROSOMA GIGANTEUM.

Throughout the whole extent of the ascidiarium, the number of ascidiozooids appears to be undergoing a constant increase, by the development of buds from those which already exist ; at least, I have not yet met with any adult ascidiozooids devoid of a more or less advanced appendage of this kind. Gemmation always takes place from that part of the middle of the hæmal side of the body of the ascidiozooid, which lies opposite the bend of the intestine and between the posterior extremity of the endostyle and the reproductive organs. At first, therefore, the bud is situated near the posterior or cloacal end of the body, and on the same side as the closed apex of the ascidiarium.

Gemmation does not take place in *Pyrosoma*, as in so many of the lower animals (*e.g.* the *Hydrozoa* and *Polyzoa*, or *Salpa* and *Clavelina* among the Ascidians), by the outgrowth of a process of the body-wall whose primarily wholly indifferent parietes become differentiated into the organs of the bud, but, from the first, several components, derived from as many distinct parts of the parental organism, are distinguishable in it, and each component is the source of certain parts of the new being, and of these only. Thus the body-wall or external tunic of the parent gives rise to the external tunic of the bud ; while a process of the endostylic cone of the parent is evolved into the alimentary tract of the bud, and the reproductive organs of the latter are furnished by a part of that tissue whence the reproductive organs of the parent took their origin.

Pl. XXX. [Plate 29] fig. 14 represents the condition of what I may term the gemmiparous region of the body in a young ascidiozooid, in which no distinct trace of a bud is discernible externally. The outer tunic, it will be observed, passes evenly backwards, and has the same structure in the situation of the future bud as elsewhere. The endostyle is continued upwards and backwards as a cellular cord, which contains a cavity continuous with the groove of the endostyle, is about $\frac{1}{1200}$th of an inch thick, and is rounded-off at its extremity. From this a thin sheet of indifferent tissue is continued downwards and backwards, so that its plane forms nearly a right angle with the direction of the end of the endostyle, and suddenly thickens to $\frac{1}{710}$th of an inch. After this it tapers off gradually to its extremity, which lies

free in the cavity of the blood-sinus, at a distance of $\frac{1}{130}$th of an inch from the ovisac of the ascidiozooid, which is $\frac{1}{210}$th of an inch in diameter, and so far advanced that there can be no question as to its real nature. The total length of this mass (which, for reasons which will shortly appear more fully, I have termed the *generative blastema*) is [illegible]nd of an inch; and for the greater part of its extent it has the character of indifferent tissue. But the sudden enlargement to which I have referred is occupied by a body which has all the characters of an ovum, consisting of a structureless yelk $\frac{1}{640}$th of an inch in diameter, and of a clear germinal vesicle ($\frac{1}{1200}$th), enclosed in which is a germinal spot ($\frac{1}{1800}$th). It will appear by-and-by that this is, in fact, the solitary ovum (surrounded by its rudimentary ovisac) which will come to maturity in the bud to be formed at this spot; and it is not a little remarkable that the first recognizable part of the new organism should be the foundation of that structure which will eventually develope into a creature distinct from it.

In fig. 15 a more advanced condition of a bud is depicted; the backward continuation of the endostylic cone is broader, more distinctly hollow, and is so bent up as to form a more acute angle, both with the line of direction of the endostyle and with the plane of the generative blastema. In consequence of this change, and of the general enlargement of the parts, they can no longer be contained within the blood-sinus, whose outer wall is now elevated into a conical cap which fits over the conjoined ends of the process of the endostyle and the generative blastema. That part of the external tunic which constitutes this cap is thickened, and exhibits the texture of indifferent tissue. The ovum in the generative blastema is now very distinct, and the tissue around it is so disposed as to mark out the walls of an ovisac which measures $\frac{1}{480}$th of an inch in diameter. The clear germinal vesicle measures $\frac{1}{800}$th of an inch; and its spot has the same diameter as before. Behind the ovisac, which occupies the greater part of the cavity of the diverticulum constituting the bud, a distinct constriction marks off the rest of the generative blastema, which lies closely connected with the external tunic of the parent, and altogether excluded from the cavity of the "cap" of the nascent bud. It is now no longer taper, but cylindrical and rounded at the end; and near its anterior extremity a new germinal spot, surrounded by a small clear vesicle, is visible.

Fig. 16 represents a bud $\frac{1}{320}$th of an inch broad by $\frac{1}{480}$th of an inch high. The process of the endostylic cone is very distinctly hollow and somewhat thin-walled, while its axis is nearly parallel with that of the bud. In fig. 17, the bud, now subcylindrical, has

increased in length to $\frac{1}{192}$nd of an inch; and the front view of a similar bud, given in fig. 18, shows that the hollow process of the endostylic cone is slightly constricted in the middle, and that the interval between its walls and the external tunic is occupied by a granular mass.

In fig. 19, a marked advance is discernible. The bud is distinguishable into a body or rudimentary ascidiozooid $\frac{1}{112}$th of an inch long, and a much shorter stalk or peduncle. The ascidiozooid is broad at its attached end, more or less tapering at its opposite extremity. Its external tunic is distinct, but proportionably thinner than before, and is continued into the outer wall of the peduncle and thence into the external tunic of the parent. The hollow process of the endostylic cone is about as broad as before, in the peduncle; but after traversing this, nearer its anterior than its posterior side, it suddenly dilates into a pyriform sac, somewhat similar in contour to the rudimentary ascidiozooid itself. The upper taper end of this sac seems to be attached to the inner surface of the apex of the outer tunic of the ascidiozooid. Anteriorly and posteriorly, its walls appear thick, the enlargement being much more marked posteriorly. The side of the sac turned towards the eye, between these thickenings, exhibits five faint rings, with comparatively clear centres. In order to avoid circumlocution, I may so far anticipate the results yielded by the investigation of later stages of the buds, as to state the nature of the parts which have now been described. The rings are the indications of the commencement of as many branchial stigmata; the anterior apparent thickening is the result of the formation of the rudiment of the endostyle; the posterior apparent thickening is produced by the rudiment of all that part of the alimentary tract which lies behind the branchial sac, into which almost the whole of the dilated end of the prolongation of the endostylic cone is converted. A comparatively clear space surrounds the apex of the branchial sac, below which the inner surface of the external tunic presents a band-like aggregation of indifferent tissue, the rudiment of a body which corresponds with what Krohn has called the elæoblast in the *Salpæ*; and finally, projecting from the posterior wall of the external tunic, and apparently connected with the elæoblast, is an elongated mass, the anterior portion of the generative blastema, which has now become completely separated from the posterior part. The anterior end of the latter, in fact, extends only into the peduncle, while its posterior moiety lies, attached to the outer tunic of the parent, in the great hæmal blood-sinus. The generative blastema may therefore be now distinguished into three parts—parental, peduncular, and gemmular

—of which the two former remain connected, until a new bud is developed in the distal end of the peduncle, while the latter, now contained wholly within the bud, and separated from the others by a considerable interval, is itself divisible into three portions. The first of these is the ovum, or rather ovisac, larger and more distinct than in the last-mentioned stage; the second is that part of the blastema near this, which will become the testis, but which, at present, has no definite form; and the third is represented by a slender band of indifferent tissue continued up to the apex of the branchial sac (the future extremity of the endostylic cone), which is the generative blastema of the nascent ascidiozooid and will supply reproductive organs to its buds. The interspace between the branchial sac and the outer tunic of the bud is in free communication with the blood-sinus of the parent, by means of the interval between the endostylic cone and the wall of the peduncle; and, in fact, this interspace is itself the foundation of all the blood-sinuses of the bud.

This is as much as can be clearly made out from the inspection of side views of buds in this and earlier stages; but much additional information is to be gained from other views of similar buds. Fig. 26 exemplifies the appearances yielded by a bud about $\frac{1}{192}$nd of an inch in diameter, when seen from above.

The transverse section of the wide sac-like prolongation of the endostyle thus presented to the eye is four-sided; the lateral and posterior walls are concave, while the middle of the anterior wall is produced into a sort of fold; so that the contour of the sac may be compared to that of a crown. Masses of indifferent tissue fill the interspace between the concavity of the lateral wall of the sac and the sides of the external tunic, while the interval between the posterior wall and the hinder part of the external tunic is nearly filled up by the young ovisac. Fig. 27 represents an advance upon this condition, —the two principal changes to be noted being, first, the conversion of the lateral masses of indifferent tissue into hollow oval bodies containing a very small cavity, and, secondly, the prolongation of the posterior cornua of the alimentary sac.

It is obvious that if either of these buds were viewed sideways, the middle fold of the anterior face of the sac would appear like an anterior thickening, while the posterior prolonged cornua would simulate a posterior enlargement, and the whole would closely resemble fig. 19; and it now becomes important to prove, by the study of more advanced stages, the nature of the sac, of its anterior median fold, of its posterior cornua, and afterwards of the lateral sacs. Fig. 28 represents a larger bud, which presents more of its anterior

than of its upper, aspect to the eye. The anterior fold, consequently, is represented by only two dark streaks with a clear interval. The posterior cornua are more elongated than before. There is a rounded opaque spot at the anterior end of the bud. In fig. 29, the dark streaks have become the middle bands of the endostyle; the anterior spot is obviously the nascent oral aperture; while the posterior cornua have become separated from the rest of the cavity of the sac, communicating with it by only a small aperture. The cornua are, at present, of equal size; but in fig. 30 the left cornu exhibits a trihedral dilatation, which is obviously the commencement of the stomach, while the right cornu and the part which joins it with the left have become, the latter the foundation of the arch of the intestine, and the former of the rectum. There can be no doubt, therefore, that the greater part of the sac into which the prolongation of the endostyle is developed becomes what would in other animals be called the pharynx, namely, that portion of the alimentary canal which lies between the œsophagus and the mouth [1].

Side views, such as those given in figs. 20 & 21, of buds, in similar stages of development, are equally instructive. The attached apex of the sac is seen to become the posterior end, or cone, of the endostyle. The small size of the gastro-intestinal, in proportion to the pharyngeal portion of the alimentary tract, and the free communication of the latter with the prolongation of the endostylic cone of the parent, which traverses the peduncle, are clearly seen; and I entertain no doubt that, by means of the last-mentioned communication, the cavity of the pharynx (or, as we shall see it becomes, that of the branchial sac of the bud) is placed in communication with that of the parent. In favourable lateral views of buds in this stage, it is easily made out that the wall of the pharynx unites with the external tunic at its anterior end, and here gives rise to the oral aperture, whose tentacular fringe is only subsequently developed.

Having traced the fate of the sac-like dilatation of the prolonged portion of the endostyle thus far, I will now direct the attention of the reader to the coincident progress of the lateral sacs, or oval hollow bodies, as I previously termed them. In fig. 27 they are very small and thick-walled; in fig. 28 their cavity is larger, their walls are proportionally thinner, and the sacs themselves are both absolutely

[1] The development of the Ascidian pharynx, as traced out by Krohn in *Phallusia*, and by myself in the present memoir, appears to me to afford ample demonstration of the justice of Milne-Edwards's view, that the branchial sac of the Ascidian is the homologue of the pharynx of the Polyzoon. It is due to my friend Prof. Allman, however, to refer to what he has said in support of another theory, in his able essay "On the Homology of the Organs of the *Tunicata* and the *Polyzoa*," Transactions of the Royal Irish Academy, vol. xxii.

and relatively larger. In fig. 29 they are very much larger and thinner, and their relations to other organs are especially worthy of attention. The outer layer of each is applied to the outer tunic of its side, leaving a small interspace, which communicates freely with the great posterior sinus, in which the intestine and genitalia are disposed, and with the anterior sinuses which lie between the pharyngeal wall and the external tunic. This interspace is, in fact, the parietal sinus. The internal layer, continuous with the outer anteriorly and posteriorly, but separated from it by a wide chamber for the rest of its length, is applied against the wall of the pharynx for four-fifths of the extent of the latter, and then coats the lateral portions of the gastro-intestinal tract, forming the antero-lateral boundary of the great posterior sinus. The space between the wall of the pharynx and the inner layer of the sac communicates anteriorly with the anterior sinuses, posteriorly with the posterior sinuses, and it is interrupted at several points by the union of the pharynx and inner layer with one another. It represents the system of branchial sinuses.

In side views it is not easy to make out the boundaries of the lateral sacs; but it is most important to observe that, as has been already mentioned, in the middle of the lateral face of the pharynx, and, therefore, also in the middle of the lateral face of the inner wall of the sac, a series of opaque rings with clearer centres, the rudiments of the branchial stigmata, make their appearance (figs. 19 and 20). These correspond with the points of union of the pharynx and the inner wall of the sac. They are, at first, small, round, and very indistinct, but, by degrees, they elongate in a direction perpendicular to the long axis of the pharynx, and their real nature becomes apparent. Hence it is clear that these stigmata must eventually open into the lateral sacs, as indeed they may be seen to do in such buds as that represented in fig. 30; and hence also it follows, that the lateral sacs are the rudiments of the lateral atria.

At first the lateral atria appear to be perfectly distinct from one another, and no atrial aperture is discernible. In buds such as that represented in fig. 29, again, they do not extend, posteriorly, further than the sides of the alimentary canal; but in more advanced buds (fig. 30) they are produced backwards on each side until they pass beyond the level of the posterior margin of the stomach, so that they now constitute the entire lateral boundaries of the great posterior sinus. The longitudinal section (fig. 21) of a somewhat smaller bud than that represented in fig. 30 shows, however, that, in this condition, the atria are no longer distinct, but are united together below the

stomach by a comparatively narrow and short canal (*p*), which is the mid-atrium.

I have not traced out all the details of the process of coalescence of the lateral atria; but I suppose that each branchio-parietal portion of the atrium, at first a distinct sac, is prolonged downwards and inwards, under the stomach, and that the opposed walls of the prolongation become applied to one another, coalesce, and then become perforated. At any rate, the mid-atrium is now surrounded by a membranous wall, continuous on all sides with the lining of the lateral atria, and applied superiorly and anteriorly against the stomach and œsophagus, posteriorly and inferiorly against the external tunic, but not touching either of these parts, except for a small space on the floor of its chamber, where it becomes united with the external tunic to allow of the formation of the atrial aperture. In the present bud (fig. 21) this aperture is situated on the neural side of the body, in front of the posterior end, which is chiefly occupied by the genitalia; but as development goes on, the mid-atrium increases disproportionately, and encroaches upon the other organs, upwards and forwards, in such a manner that its anterior wall invests the whole posterior and lateral faces of the gastro-intestinal division of the alimentary canal; while its roof (to speak metaphorically) thrusts the genitalia altogether into the hæmal region of the body, and its posterior and inferior walls, extending backwards, carry the external tunic with them, and eventually cause the atrial aperture to take its place at that extremity of the body which is directly opposed to the mouth, and far behind the genitalia (see figs. 22–25).

The communicating apertures between the mid-atrium and the lateral atria increase in size *pari passu* with the growth of the parts; and hence, in the fully formed ascidiozooid, the gastro-intestinal division of the alimentary canal is enclosed in a sort of vertical mesentery (formed by the anterior wall of the mid-atrium in the middle line, and the internal wall of the lateral atria at the sides), whose layers are continued, on either hand, into the outer wall of the branchial sac. At the anterior boundary of the branchial sac they are reflected into the outer or parietal layer of the lateral atrium.

The facts which I have detailed[1] are exceedingly important for the comprehension of Ascidian structure in general. From its mode of development, it is perfectly obvious that the inner wall of the branchial sac of *Pyrosoma* is not composed of tentacles which have

[1] The accurate Krohn, in his account of the development of *Phallusia* (Müller's "Archiv," 1852), was the first to note the separate origin and subsequent confluence of the lateral atria. In this genus, however, each lateral atrium has, at first, a distinct external aperture.

coalesced, but that it is, originally, a simple imperforate dilatation of the pharyngeal portion of the alimentary canal. The development of the atrium adds a second or outer wall to this dilatation; and when, by the formation of this double wall, the branchial sac is constituted, the stigmata make their appearance in its parietes—the atrial and the pharyngeal walls becoming united around the margins of each stigma.

When a bud has attained a length of between $\frac{1}{17}$th and $\frac{1}{35}$th of an inch, the narrow neck connecting it with the peduncle is obliterated, and it lies free in the general test of the parent ascidiarium. It next elongates until its oral and atrial apertures are placed in connexion with the exterior and the cloaca respectively (the latter connexion appearing to be effected first), and then it increases in depth until it acquires the appearance of the adult. Before it is detached, however, the portion of the peduncle nearest it enlarges and assumes the shape of a new bud; so that the proximal end of the peduncle now passes into a small bud with whose apex a larger one is connected (fig. 22). And I suspect that this process is repeated as long as there is any reserve of generative blastema in the parental organism. I have, however, never actually seen more than two buds thus connected together. As the buds are all developed from the hæmal region of the pre-existing ascidiozooids, it follows that the new ascidiozooids formed by gemmation must at first be thrust among the old ones, towards the apical end of the ascidiarium.

So much in elucidation of the mode in which the buds attain the form and general arrangement of organs characteristic of the adult. I now proceed to speak of such among the minor changes which these organs undergo as call for particular remark.

Of the outer tunic all that requires to be said is, that it becomes relatively thinner as development goes on. In buds which are situated within a certain distance of the open end of the ascidiarium, and which have attained a length of $\frac{1}{17}$th of an inch (fig. 24), the outer tunic of the neural wall of the atrium is raised into a slight rounded projection (r^2), and in older buds (fig. 25) this gradually elongates, and extending towards the open end of the ascidiarium, and finally into the lip of the cloacal aperture, becomes converted into one of the stolons of the test.

The atrial muscular bands are visible in buds not more than $\frac{1}{30}$th of an inch in length (fig. 23); the pharyngeal muscular bands, only in more advanced zooids.

The tentacular fringe appears first as an inward thickening of the parietes of the mouth. The hæmal tentacle is markedly the longer,

even in such buds as that represented in fig. 24. The ganglion is discernible in buds $\frac{1}{70}$th of an inch long (fig. 20) as an opaque oval mass situated between the peduncle and the oral end of the bud, and very much larger in proportion to the rest of the organism than afterwards. The ciliated sac appears as a short cæcal diverticulum of the pharyngeal cavity, connected with the anterior and hæmal side of the ganglion.

A most curious structure is visible in buds $\frac{1}{70}$th of an inch long, and remains obvious until they have attained a length of $\frac{1}{20}$th of an inch or thereabouts. For want of a better name, I will term this the 'diapharyngeal band.' In the section, fig. 21, its upper part is visible, passing obliquely downwards and backwards from between the two middle bands of the endostyle; while, in figs. 22 & 23, its lower extremity is seen to end in the pharynx, immediately over the posterior moiety of the ganglion. The diapharyngeal band is hollow, and effects a communication between the hæmal and neural sinuses; and if, as is possible, the heart of the bud has at this period but little functional activity, the existence of this direct channel may facilitate the circulation of the blood. However this may be, this structure becomes longer and thinner as the development of the bud advances; and all that remains of it, in buds $\frac{1}{17}$th of an inch long (fig. 24), is a small tubercle which lies over the posterior part of the ganglion. Eventually even this disappears.

I have already spoken of the origin of the branchial stigmata. Fig. 21 represents an accidental, but very fortunate, longitudinal section of a bud $\frac{1}{70}$th of an inch long; the razor having passed rather to the right of the middle line above, rather to the left below. As it is seen from the right side, the inner surface of the left wall of the branchial sac is exposed to view. Of the eleven stigmata, those in the middle are the longest and most oval, those at the two ends of the series shortest and most rounded. They look clear in the centre, but on careful examination they are seen to be closed, the sheet of indifferent tissue which forms the innermost wall of the pharynx being continued over them. I am strongly inclined to think that it is this sheet of indifferent tissue which gives rise to the longitudinal branchial bars, for in more advanced buds (fig. 22), in which the median stigmata have undergone much elongation, the same layer is continued over their hæmal and neural ends, while it has disappeared in the interval, except along three longitudinal lines, where it evidently forms the foundation of as many longitudinal branchial bars. In the more advanced stages, new stigmata are added to the anterior and posterior ends of the series. Those already formed elongate, and new

longitudinal bars are added, until the walls of the branchial sac assume their perfect form[1].

As I have explained, the sac-like alimentary tract originally ends in a conical point at that extremity which is opposite its oral end; and this cone is connected with the external tunic. In subsequent stages the cone remains distinct, being directed at an obtuse angle to the rest of the hæmal wall of the pharynx, while the cellular bands which eventually render the endostyle so conspicuous, cease at its base. It, at first, communicates by its widely open base with the pharyngeal or branchial cavity; but as development proceeds, it becomes narrower, in proportion to the endostyle, and at length is represented by that slender backward prolongation of the endostyle or 'endostylic cone' described at the commencement of this memoir and represented in fig. 14.

The languets do not appear till development has advanced a long way; in fact, in the very young buds there is no room for them, as almost all the space between the place of the commencement of the œsophagus and the place of the ganglion, is occupied by the aperture of communication between the prolongation of the endostylic cone and the pharynx. As growth proceeds, the distance between the ganglion and the œsophageal aperture gradually increases, both absolutely and relatively, and in buds $\frac{1}{30}$th of an inch long, one or two small tubercles are visible, projecting from the hypopharyngeal band, between the œsophageal aperture and that of the canal which traverses the prolongation of the endostylic cone. These gradually increase in number, elongate, and assume their adult shape and size (figs. 24, 25).

The figures will sufficiently explain the further changes of form undergone by the gastro-intestinal portion of the alimentary canal.

The hepatic tubular system makes its appearance in such buds as that represented in fig. 22, as a minute diverticulum of the stomach, which elongates, applies itself to the intestine and ramifies over it. Krohn (*l. c.* p. 331) saw it originate in a similar manner in *Phallusia*.

The heart, similar to that of the adult in form and texture, is distinctly discernible in buds not more than $\frac{1}{30}$th of an inch long, attached, in its ordinary position, to the wall of the pharynx, just in front of the bend of the intestine, between it and the endostylic cone. I have not been able to trace out the first condition of this

[1] Krohn (*l. c.* pp. 324 and 327) states that the stigmata of the embryo *Phallusia* make their appearance as round apertures; but he affirms that new ones are added, not only in front and behind, but in the neural and hæmal sides of the first formed series.

organ and the changes which it undergoes in acquiring the state now described.

The renal organs are plainly visible in buds not more than $\frac{1}{50}$th of an inch long as aggregations of clear, round, almost colourless corpuscles, between the atrial and the outer tunic.

In describing the first stage of the bud (fig. 14), I have spoken of a thin layer of indifferent tissue which passed from the end of the endostylic cone, or prolongation, into the generative blastema. In more advanced stages, this tissue forms a sort of hood over the end of the saccular rudiment of the alimentary tract (figs. 15 and 16), and seems to be the means of connecting the end of that sac with the external tunic.

After a time, however, a clear space appears around the apex of the sac, and separates this connecting mass from the rest, which now, consequently, appears as a broad zone (*a*) surrounding the sac below its apex, but above the uppermost of the branchial stigmata (fig. 19), This zone remains as a broad, thickish girdle of indifferent tissue closely connected with the outer tunic externally and in front, and with the generative blastema behind, in buds of $\frac{1}{70}$th—$\frac{1}{50}$th of an inch long (figs. 21 and 22); but in larger zooids its tissue has undergone a great change, and it has become a transparent mass, through which ramified corpuscles, like connective-tissue corpuscles, appear scattered (fig. 23). In this condition it is exactly analogous to the structure termed elæoblast in the *Salpæ* by Krohn. Its bulk is now equal to a fifth or a sixth of that of the entire bud, but in subsequent stages (figs. 24, 25) it diminishes both absolutely and relatively in size and eventually it disappears.

In buds $\frac{1}{50}$th of an inch in diameter, the generative blastema remains in its primitive condition, except that it and the ovisac it contains, have increased in size. Its anterior pointed end is closely juxtaposed to the endostylic cone. In the zooid represented in fig. 23, which measured $\frac{1}{30}$th of an inch in length, the generative blastema has become divided into two parts, the smaller of which remains in close apposition to the endostylic cone, while the larger, retaining its connexion with the posterior and upper wall of the mid-atrium, becomes widely separated from the other. The interval between the two is occupied by the elæoblast. Even before the separation has taken place, the larger portion has become distinctly differentiated into two parts, the ovisac, on the left, separating itself from a rounded mass of indifferent tissue, on the right. This last is the rudiment of the testis. From rounded, it becomes pyriform, the narrowed neck of the pear remaining in connexion with the atrial wall, and eventually

becoming metamorphosed into the vas deferens, while the broad end increases in size, and is directed more forwards as well as upwards.

In a bud $\frac{1}{17}$th of an inch long (fig. 24) the testis measures $\frac{1}{380}$th of an inch in length, while its broad end is above $\frac{1}{500}$th of an inch thick. The apex of the vas deferens already pushes a little eminence of the atrial tunic before it.

In a young ascidiozooid, somewhat more advanced than that represented in fig. 25, the vas deferens is $\frac{1}{380}$th of an inch in length, and is of nearly even diameter throughout, except at its upper end, where it is slightly dilated and plainly hollow. It is connected with the posterior part of the terminal enlargement, which is nearly $\frac{1}{200}$th of an inch thick, and is divided into three short lobes, each about $\frac{1}{500}$th of an inch thick. Like the previously existing pyriform enlargement, these rudimentary cæca are solid masses of indifferent tissue. Traces of a distinct membrana propria are discernible around each cæcum. In still larger ascidiozooids the number of cæca increases, and the whole organ becomes larger, until it assumes its adult form; and it is only when nearly in this condition, that spermatozoa are visible in the vas deferens and the adjacent parts of the cæca.

The development of the ovisac will be described below. At first both the testis and the ovisac have ample room within the sinus of the zooid in which they are lodged; but as they increase in size, the duct of the ovisac extending towards the neural side and forwards, and the duct of the testis extending towards the neural side and backwards, push the atrial tunic before them, so that their openings are eventually situated on slight papillary elevations. The principal portions of the two organs, on the other hand, consisting of the sac of the ovisac and the cæca of the testis, as they enlarge, pass into chambers in the test, which are formed for them by the recession of the outer tunic, and whose cavities, consequently, communicate freely with the hæmal blood-sinuses.

With respect to that part of the generative blastema which remains in connexion with the endostylic cone, one of its endoplasts or nuclei soon acquires a larger size, and becomes surrounded by a clear space, thus giving rise to a new germinal vesicle and spot, round which will eventually be formed the solitary ovum and ovisac of a new bud, developed from the zooid, whose origin has just been traced, in exactly the same way as itself has arisen.

Thus, if we start with a single ascidiozooid, it may give rise, to all appearance, to an indefinite succession of buds, by successive enlargements and detachments of the end of the peduncle of the first; and each bud thus developed carries within itself, in its generative

blastema and endostylic cone, provision for an indefinite succession of other buds. It must be recollected, however, that while the tissue of the rudiments of the alimentary and reproductive systems of each bud is directly descended, with comparatively little alteration, from the blastoderm of the embryo *Pyrosoma*, yet this tissue cannot be said to be embryonic ; the tissue of the endostylic cone being considerably differentiated, while the outer tunic of each bud is derived from the still more modified outer tunic of the parent ascidiozooid. These facts, therefore, lend no countenance to the doctrine, whose fallacy I have demonstrated in a previous memoir, that budding depends on a retention of the primitive tissue of the germ in any part.

§ 4. *The Gamogenesis, or Sexual Development, of* PYROSOMA GIGANTEUM (Plate XXXI. [Plate 30]).

It will conduce to intelligibility, if the somewhat complex history of this process is divided into stages, characterized partly by the size of the ovisac, partly by its structural characters. I shall describe, under each stage, a specimen or specimens, illustrating the peculiar features of that stage, but it will be understood that insensible gradations are observable between the different stages ; and, in order that the whole process of development may be viewed continuously, it will be advisable to consider, as the first stage, that condition of the ovisac in which it is first recognizable as a completely distinct organ, a condition which it attains, as I have already stated, in buds such as that figured in Pl. XXX. [Plate 29] fig. 23.

First Stage. *Ovisacs less than $\frac{1}{350}$th of an inch in diameter and without ducts.*

Fig. 1, Pl. XXXI. [Plate 30], represents an ovisac measuring $\frac{1}{420}$th of an inch in diameter. It is ellipsoidal in form, and nowhere presents any prolongation which can be regarded as even the rudiment of a duct. The wall of the ovisac is comparatively thick, and obscurely cellular in structure, but it is devoid of any structureless investment or membrana propria. The contained ovum consists of a solid-looking, well-defined germinal spot $\frac{1}{2700}$th of an inch in diameter, occupying the centre of a germinal vesicle $\frac{1}{800}$th of an inch in diameter, with a thin but well-defined wall, and perfectly clear contents. The yelk is represented by a small zone of structureless, yellowish substance, which invests the germinal vesicle, and, on the one hand, passes into the wall of the ovisac, while, on the other, it is separated from that wall by a narrow clear space.

Second Stage. *Ovisacs less than $\frac{1}{200}$th of an inch in diameter and unimpregnated.*

The ovisac represented in fig. 2. exemplifies this condition very well. It has a diameter of $\frac{1}{300}$th of an inch. Its form is spheroidal, and it is produced on the side towards the atrial wall of the blood sinus in which it lies, into a short subcylindrical diverticulum, which is directed forwards, and slightly towards the neural side of the ascidiozooid in which it lies. This diverticulum, or rudimentary duct, is [illegible]th of an inch in length, and its slightly narrowed anterior extremity passes into the atrial tunic. At its opposite end, where it becomes continuous with the ovisac, it measures $\frac{1}{970}$th of an inch in diameter. At this extremity, the cavity of the duct is in free communication with that of the ovisac, but at a little more than half way towards the opposite end, or in other words towards the atrium, the cavity ceases, the termination of the duct appearing to be a solid cellular mass. In this condition, therefore, there would appear to be no communication between the interior of the ovisac and the atrial cavity.

The wall of the ovisac exhibits no distinct membrana propria, but is composed of a single layer of flattened corpuscles, about $\frac{1}{5000}$th of an inch in diameter, imbedded in, and connected together by, a structureless substance. The wall of the duct is similarly composed, but its hæmal is much thicker than its neural wall. In the cavity of the duct nothing save a clear fluid is discernible, and the same fluid seems to fill the interval observable on one side, between the wall of the ovisac and the ovum.

The latter consists of a very finely granular, spheroidal vitelline mass [illegible]th of an inch in diameter, within which lies a germinal vesicle ([illegible]th) with perfectly clear contents, inclosing an opaque, spheroidal, germinal spot ($\frac{1}{1920}$th). The yelk is in close contact with the inner side of the anterior wall of the ovisac—the germinal vesicle is close to its surface at the same point, and the germinal spot is applied to the inner surface of the anterior wall of the vesicle, so that it is as near as possible to the wall of the ovisac.

I have not been able to discover a trace of a vitelline membrane in ova in this stage. It may be doubtful whether the space between the wall of the ovisac and the ovum is a natural or an artificial product. My observations upon the ovisacs of a fresh *Pyrosoma* (Phil. Trans. 1851) lead me to adopt the latter hypothesis.

Third Stage. *Ovisacs under $\frac{1}{100}$th of an inch in diameter and in process of impregnation.* (Pl. XXX. [Plate 29] figs. 3, 4, and 8*.)

Of the two specimens in this stage which I have figured, the larger (fig. 3) is rather the less advanced. Its duct is longer than the diameter of the ovisac, and is not only hollow throughout its whole length, but, at its anterior end, opens into the atrium, with which, therefore, its cavity is in free communication. Whether a similar connexion obtains between the cavity of the ovisac and that of the duct, or not, I cannot certainly say. A marked constriction is generally observable at the point of junction between the duct and the ovisac, corresponding to an inwardly projecting lip, which greatly narrows the apparent aperture of communication (fig. 4); and in some cases, the cellular wall of the lip appeared to have grown out, in such a manner as still further to diminish that aperture; but I have been unable, in any one instance, fully to assure myself of the closure of the passage. If, however, as I have reason to believe, the vitellus, in the fresh state, completely fills the ovisac, the aperture will be effectually closed by its means.

The ovum in the ovisac represented in fig. 3, measures $\frac{1}{192}$nd of an inch in diameter, that in fig. 4, $\frac{1}{210}$th. In each case the vitellus is somewhat more opaque than in the previous stages; but, as before, I have been unable to find any vitelline membrane, even when, as in fig. 8*, the ovum has been turned out of the ovisac. But I have constantly observed that while the greater part of the circumference of the yelk exhibits a well-defined dark contour, that portion which is away from the side on which the germinal vesicle lies, has a faint, hazy outline, as if it were undergoing solution. This appearance is well shown in figs. 4 and 8*, and it is worth recollecting in connexion with the subsequent fate of the yelk.

In both the ova represented in figs. 3 and 4, the germinal vesicle measures $\frac{1}{480}$th of an inch in diameter, and its contents are, as before, perfectly clear. A change of figure has accompanied its increase in size, for it is now oval, its long diameter being more or less perpendicular to the direction of the duct. Furthermore, it is situated at the surface of the ovum, at a point close to, but on one side of, the aperture of the duct; and that face which is nearest the surface of the vitellus is not unfrequently flattened.

The germinal spot retains its previous size ($\frac{1}{1920}''$) and appearance. One or two minute clear spaces are to be seen in it, occasionally, in this and in other stages, but I suspect they are accidental.

In the specimen represented in fig. 3, the duct appears to contain

only a clear fluid, as before, except that a few indistinct striæ are visible towards its upper end. One would hardly know what to make of them, if it were not for the circumstance, that a bundle of minute filaments, a few of which would readily give rise to the striation in question, hangs from the mouth of the duct. The filaments are sticking in its atrial aperture by one end, while the remainder of their length protrudes.

The filaments are exceedingly delicate, and so entangled that their individual dimensions cannot be estimated. The whole bundle, however, measures about $\frac{1}{130}$th of an inch in length. The ends of the filaments inserted into the aperture are thickened, and more or less rod-like. In a slightly larger ovisac (fig. 4) no such filaments are visible about the mouth of the duct, but its upper dilated end contains a conical plug, composed of precisely similar bodies, and a similar plug occupied a corresponding position in every other ovisac, in this stage, which I have examined. If the ovisac is not disposed in such a manner, that the plane of the constricted junction between the duct and the ovisac is perpendicular to the stage of the microscope, so as to afford a true profile view, the broad end of the plug will appear to be in direct contact with the vitellus, close to the germinal vesicle. But I have never met with any such absolute contact in a true profile view. On the contrary, in such a view, the end of the plug appears to be jammed in the upper aperture of the duct, and there is a small interval between it and the surface of the vitellus.

But it must be remembered that (as I have already pointed out) in the fresh state, the vitellus, in all probability, occupies the whole cavity of the ovisac, and itself stops the upper aperture of the duct; and, if this be the case, it is exceedingly likely that the slight separation between the yelk and the plug of filaments is a post-mortem change. At any rate no filaments are ever discoverable in the cavity of the ovisac, and as I have been able to find no complete diaphragm across the upper aperture of the duct, there seems to be no reason for their absence, unless we suppose that the vitellus itself bars their entrance. But in this case the plug and the vitellus must come into direct contact.

This point is of great importance, because there can be no doubt that the filaments in question are spermatozoa. The 'plug,' and the contents of the vas deferens of the testis are precisely similar in appearance. The plug is not visible before the atrial end of the duct is open, thus providing free access for spermatozoa floating in the atrium. As there are no cilia on the inner surface of the duct, it

seems impossible to account for the presence of the dense mass of filaments within it, except on the supposition that they have an inherent propulsive power ; and the only free, filamentous bodies possessed of such a power we know of, in the animal economy, are spermatozoa.

Furthermore, in my former memoir on *Pyrosoma* (*l. c.* p. 584), I have recorded the following observation :—

"In young specimens, when the ovum is small and the yelk pale, this gubernaculum [the duct] frequently appears to be solid ; but in fully grown specimens, when the ovum [ovisac] has its full size, and the yelk is dark and granulous, it presents the appearance of a wide tube, especially at its upper part. And here, there was frequently an appearance of dark striæ and moving granules, prompting the belief that spermatozoa had travelled thus far. In one instance the sac of the ovum was empty, and the gubernaculum or duct widely distended ; the appearance of spermatozoa in the duct was here very strong. (Fig. 5.)"

I entertain no doubt, then, that the specimens described exhibit the process of impregnation in *Pyrosoma* ; that the spermatozoa make their way up the duct and come into contact with the surface of the yelk. Whether that reciprocal action of the spermatozoon and the ovum, which constitutes the essence of fecundation, takes place immediately on the occurrence of this contact, I cannot pretend to say with certainty, but I doubt it ; for, as will be seen, though very remarkable changes take place shortly after impregnation, they are not those which in other animals follow upon fecundation.

It is not a little singular that, in consequence of the immature condition of the testis of zooids whose ovisacs are in the stage under consideration (*Pyrosoma* resembling *Salpa* in the much more rapid advance towards maturity of the female, than of the male, organ, in each zooid), the spermatozoa which effect impregnation must be derived from another zooid if not from another ascidiarium. The latter alternative is not so improbable as it looks at first sight, if we consider that a current constantly sets through the body of each zooid from the oral the atrial aperture, and so out at the cloaca. Hence, the spermatozoa which are poured by the vas deferens of any given zooid, in which the testis has attained its full development, into its atrium, must be almost immediately carried into the cloaca ; and as a powerful current is setting into the cloaca from every other zooid, it does not seem possible that the spermatozoa should make their way into any one of these zooids against it. But on the other hand, as the *Pyrosomata* live in great troops, the spermatozoa cast out of the cloaca of

any one *Pyrosoma* may very readily be taken in by the oral aperture of another, and passing with the current through the branchial stigmata into the atrium, may easily reach the aperture of the oviduct.

If this reasoning is valid, *Pyrosoma* affords a curious illustration of Mr. Darwin's doctrine of the rarity of self-fertilization even among hermaphrodite animals.

Fourth Stage. *Ovisacs from $\frac{1}{100}$th to $\frac{1}{40}$th of an inch in diameter, in which the yelk disappears and the germinal vesicle becomes fixed to the wall of the ovisac.* Figs. 5—8*a*.

Figure 5 represents an ovisac $\frac{1}{90}$th of an inch in diameter, and fig. 6 another of $\frac{1}{70}$th of an inch. The first thing to be observed about these ovisacs is, that they have increased in dimensions disproportionately to their ducts; for while, in the preceding stage, the duct is longer than the transverse diameter of the ovisac, in the present stage, it, at first, hardly equals, and subsequently remains much shorter than, that diameter. The duct, in fact, does not attain a greater length than $\frac{1}{150}$th of an inch, and in the larger examples of this stage it appears shrunken and withered. The spermatozoa, however, are always visible in its upper dilated end (fig. 6 *b*), but sometimes they no longer form a distinct bundle, but appear scattered, and then their rod-like heads are very distinct.

In the wall of the ovisac and of the duct, a differentiation has taken place into an outer structureless membrana propria, and an inner epithelial layer. The latter is pale, the corpuscles, which lie in the wall of the ovisac in this as in earlier stages, appearing to be thinner and separated by wider clear interspaces. That change which arrests the attention of the observer most forcibly, however, is the entire absence in the present, as in all subsequent stages, of that vitelline mass which is so conspicuous in less advanced ovisacs. As a consequence of this disappearance of the yelk, the germinal vesicle lies apparently free and bare, in contact with one wall of the ovisac. There is not the slightest difficulty in observing these facts, nor the least ambiguity about the microscopical appearances; but the circumstances appeared so unprecedented, that, when I first became acquainted with them, I mistrusted the obvious interpretation of those appearances. However, I found, not only that the contour of the yelk contained in the smaller ovisacs was perfectly well defined, but that, by careful manipulation with needles, under the simple microscope, I could turn out the ovum entire, the vitellus being so firm

and consistent as to retain its form (fig. 8*) ; and yet I could neither observe the smallest trace of the yelk in entire ovisacs in this stage, nor, however carefully I opened them, discover any trace of yelk within them. I found, furthermore, not only that, by a little pains, I could open the ovisac so as to view the germinal vesicle from within (figs. 6 and 7), but that I could evert it, turn it in all directions, and even detach it entirely : and when I discovered, by these means, not merely that no vitellus surrounds the germinal vesicle in this stage, but that it is enclosed and held in place by something which is assuredly not vitellus, I was forced back into my original conclusion, that in this stage the vitellus, as such, has disappeared.

There is, however, one suggestion which deserves careful consideration. It may be said, that what I have termed the germinal vesicle (represented separately in figs. 6*a* & 8) is in fact the ovum. To meet this objection, I would beg the reader to compare figs. 8 and 8* ; the former of which represents the body whose nature is in dispute, and the latter an ovum which has not reached its full size, the two figures preserving the true relative proportions of the originals. It is at once obvious that the circular solid-looking corpuscle, situated towards the upper end of fig. 8, is identical in all essential respects with the germinal spot of fig. 8*, the only difference being that it is slightly larger, measuring $\frac{1}{1600}$th of an inch, while the germinal spot of the entire ovum is about $\frac{1}{1900}$. But if this corpuscle represent the germinal spot, then the only structure which corresponds with the wall of the germinal vesicle in fig. 8* is the structureless oval, membranous sac, wrinkled on one side, which encloses the germinal spot in fig. 8. This sac, it must be admitted, differs a good deal from the germinal vesicle of fig. 8*, not only in size, but in form and in contents. In the first place, it is much larger, measuring $\frac{1}{380}$th of an inch in length, while the germinal vesicle of fig. 8*, is only $\frac{1}{560}$; next, it is oval and irregular on one side ; and thirdly (and this is the most important difference), it contains a homogeneous yellowish deposit, which is especially accumulated around the germinal spot, but is absent under the wrinkled moiety of the vesicle.

All doubts as to the identification of the body (fig. 8) with the germinal vesicle and spot of fig. 8*, however, vanish when a series of ovisacs, intermediate in size between that which yielded the ovum, fig. 8*, and that represented in fig. 6, are studied. Thus in fig. 4, the unquestionable germinal vesicle is oval, and its long diameter amounts to $\frac{1}{500}$th of an inch ; while in the ovisac represented in fig. 5, in which the yelk has disappeared, the body in dispute is precisely similar to the germinal vesicle of fig. 4, except that it is a little more flattened

and a little longer ($\frac{1}{160}$th). Its contents are quite clear, and its wall is but very slightly corrugated. But no one can question the identity of this body with that represented in place in fig. 6, and separately magnified in fig. 6*a*, which has a long diameter of $\frac{1}{417}$th of an inch, whose walls are much wrinkled, and which contains a dense yellow deposit.

I have no hesitation then in regarding the body, fig. 8, which agrees in all essential respects with that represented in fig. 6*a*, as the germinal vesicle of the primitive ovum, stripped of its vitellus.

Though devoid of any vitelline investment, however, the germinal vesicle has been neither free nor bare, in any ovisac which I have examined. It is always seen to occupy one spot of the inner face of the ovisac, a little behind and to the right of the upper aperture of the duct; and when the ovisac is opened, the germinal vesicle is found to adhere to this point with considerable tenacity. It is, in fact, held in place by a continuation of the epithelial lining, which lies between it and the cavity of the ovisac—the germinal vesicle being now situated between the epithelium and the membrana propria, so that while its outer face is covered by the latter its inner face is invested by the former. All this will be rendered easily intelligible by examining the profile views (fig. 6 and 6*a*), and the view from within (fig. 7), of the germinal vesicle *in situ*.

But it has been seen that the ovum, containing the germinal vesicle, originally lay inside the wall of the ovisac, which has become metamorphosed into the epithelium, and hence it follows that the germinal vesicle, after losing its yelk, must pass through the epithelium of the ovisac. It will be recollected that the mammalian ovum becomes similarly related to the epithelium of the Graafian follicle, and that the germinal vesicle of the bird's egg in like manner passes into and through the peripheral layer of its yelk.

Throughout the present stage there is not the least difficulty in observing the germinal vesicle and its spot in the uninjured ovisac. The spot, in fact, is particularly well-defined, and immediately strikes the eye when even a low magnifying power is used. But, with such a power (say 200 diameters), it is easy to fall into error as to the shape of the germinal vesicle. It constantly appears to be hemispherical, the truncated side being that which is turned away from the upper aperture of the duct. This appearance arises from the fact that, with such a power, one sees the contents and not the wall of the germinal vesicle, and as the yellow deposit fills only that moiety which lies nearer the upper aperture of the duct, it appears like a

semicircular cake. Under a higher power (500 diameters) the wrinkled[1] membrane of the other moiety of the vesicle is always readily discernible.

Fifth Stage. *Ovisacs between $\frac{1}{40}$th and $\frac{1}{30}$th of an inch in diameter, in which the germinal spot disappears, and a number of minute granules take its place.*

The germinal vesicle, held in place on the neural wall of the ovisac, immediately behind and rather to the right of the upper aperture of the duct, in the manner which has just been described, next undergoes changes of very great interest and importance. I have devoted a very great deal of time and patience to the analysis of these changes, but it is only recently that I have felt satisfied with the results of my investigations ; and I must warn any one who is disposed to repeat these observations, that while everything which I have described up to the present moment may be demonstrated with the utmost readiness in almost any thin vertical section of the ascidiarium, the conditions of the germinal vesicle which I am about to describe occur but very rarely, and require the aid of high powers of a thoroughly good microscope for their complete elucidation. Out of a vast number of preparations which I have made, at intervals, during the last twelve months, not more than eight or nine have exhibited the exact features of which I am about to give an account.

The germinal vesicle represented in fig. 8*a*, belongs, strictly speaking, to the preceding stage. But it differs from the characteristic germinal vesicles of that stage, in that its spot has lost its solid, opaque aspect and has apparently become a vesicle with a thin, sharply-defined wall, but so pale that under a low power it would readily escape notice. Its diameter is $\frac{1}{1920}$th of an inch. The vesicle itself measures $\frac{1}{570}$th, it is much flattened, and its contents are somewhat paler than before. I have described this germinal vesicle here, because I believe that it is in that condition which constitutes the transition from the typical form of the last to the typical form of the present stage. As this last is of very great importance, I will note down the appearances presented to me by several germinal vesicles which exhibit it.

If I examine a slide, at present under my microscope, I observe, under a low power, in one place, an ovisac belonging to the fourth stage. The germinal vesicle, with its yellow contents, is very obvious,

[1] The fact that the *Pyrosoma* observed by me had been preserved in spirit should always be recollected. It is highly possible that the wrinklings are artificial.

and the round, sharply-defined germinal spot strikes the eye at once. If I now move the slide a little way, I bring into view a large ovisac about $\frac{1}{42}$nd of an inch in diameter. In this, it is only with difficulty that I can trace the outline of the germinal vesicle, and nothing is to be seen of the germinal spot. This indistinctness of the germinal vesicle does not arise from want of size or clear definition; for, if I put on a high power, I find it to have a diameter of $\frac{1}{290}$th of an inch, and its contour is perfectly well marked. The yellow deposit occupies about half its cavity as before, but it is paler; and partly on this account, and partly by reason of a further change in the structure of the epithelium of the ovisac, the vesicle is less obvious than previously. Of the germinal spot not a trace is to be seen anywhere, although the vesicle and its contents are quite transparent. Whether the contents exhibit any new structure or not cannot certainly be made out, on account of the interference of the wall of the ovisac, through which the germinal vesicle is seen. In another ovisac in this stage, also about $\frac{1}{42}$nd of an inch in diameter, the germinal vesicle, very similar to that first described, measures $\frac{1}{320}$th of an inch in length, and is half filled with the yellow deposit. No vestige of the germinal spot is to be seen, but, on that side of the contents which in earlier stages is occupied by the germinal spot, there are a number of minute, spheroidal clear granules, none exceeding $\frac{1}{10000}$th of an inch in diameter and arranged so as to form an elongated patch on the surface of the contents, the rest of which is quite free from such bodies. In another ovisac of about the same size the germinal vesicle is $\frac{1}{240}$th of an inch in diameter with pretty nearly half that thickness, and similar granules are observable upon the face of its contents, while there is nothing to be seen of a germinal spot.

But the best example of this stage is that afforded by yet another ovisac $\frac{1}{35}$th of an inch in diameter, whose germinal vesicle, $\frac{1}{350}$th of an inch in diameter, is represented in fig. 8*b*. Here the contents can be searched through and through with the greatest ease; but not the least trace of a germinal spot is discoverable, while the minute clear corpuscles $\frac{1}{10000}$th to $\frac{1}{9000}$th of an inch in diameter, scattered over the face of the contents, are exceedingly distinct. Whether they are free, or whether they are imbedded in any clear substance, I cannot say certainly, but I suspect the latter to be the case.

Putting the facts observed in this stage together, we find, that in ovisacs between $\frac{1}{40}$th and $\frac{1}{30}$th of an inch in diameter, the germinal vesicle increases in size until it attains as much as $\frac{1}{240}$th of an inch in long diameter; and that the germinal spot, as such, entirely disappears. On the other hand, on that side of the contents towards the

wrinkled part of the membrane of the germinal vesicle, a number of minute, pale, spheroidal corpuscles make their appearance and spread over the face of the contents. Considering that, as we have seen, the germinal spot becomes pale before it ceases to be visible, and bearing in mind that the power of subdivision is one of the most characteristic properties of the class of bodies to which the germinal spot belongs, I do not think it very hazardous to assume that the corpuscles in question result from the division of the germinal spot.

In all the ovisacs of this size the epithelium has undergone a very remarkable change. Instead of the thin cellular lamella which has previously lined the interior of the ovisac, a transparent substance excavated by many large spheroidal cavities of various sizes (which when the ovisac is viewed by a low power give it the appearance of being filled with numerous clear vesicles) occupies its cavity.

Sixth Stage. *Ovisacs about $\frac{1}{30}$th of an inch in diameter, in which the germinal vesicle has disappeared but a blastodermic membrane occupies its place.*

Figure 9 represents an ovisac of $\frac{1}{31}$st of an inch in diameter *in situ.* It will be observed that the duct is now very small in relation to the sac, and that the modified epithelium of the latter manifests the vesicular appearance characteristic of the later stages. The germinal vesicle is no longer to be seen, but, exactly in the position it ought to occupy, there is a patch of substance which, in profile (fig. 9), is obvious as a thick, darkish yellow line, but viewed from within or from without (fig. 9*a*) is only visible under a high power, in consequence of the excessive paleness and delicacy of its components. It is, in fact, a very thin membrane $\frac{1}{160}$th of an inch long and about half as wide, composed of a single layer of spheroidal, or more or less polygonal, corpuscles, each of which has an average diameter of $\frac{1}{1900}$th of an inch, though some are smaller and some are larger. Every one of these contains in or near its centre a small, apparently vesicular, more strongly refracting and hence more conspicuous body, usually not more than $\frac{1}{9600}$th of an inch in diameter, but sometimes attaining to fully twice this diameter. That margin of this membrane which is turned towards the upper aperture of the duct (fig. 9*a*) is tolerably sharply defined, and has an evenly curved contour, so that this extremity of the patch has almost a semicircular outline. The rest of the membrane, on the other hand, has an elongated, irregular form, and less distinctly defined edges.

In another ovisac $\frac{1}{37}$th of an inch in diameter, there is the same entire absence of the germinal vesicle and the same presence of a delicate membrane of precisely the same characters, but not more than $\frac{1}{192}$nd of an inch in long diameter and $\frac{1}{240}$th of an inch wide. In this specimen the edge of the membrane which is turned towards the duct is still more distinctly semicircular, and it is almost as well-defined as the edge of the germinal vesicle in its latest condition, though no distinct membrane is discernible. The irregular part of the membranous disk bears a smaller proportion to the semicircular part, than in the preceding case.

In each instance the membranous disk, which has been described, lies between the modified epithelium and the membrana propria. In position, therefore, it exactly corresponds with the germinal vesicle; its colour, when the light passes through a thickness of it sufficient to give colour, is exactly that of the contents of the germinal vesicle; the diameter of the semicircular portion is but very slightly greater than that of the germinal vesicle in its later stages; and finally, the minute bodies which occupy the centre of each component corpuscle of the membrane are not a little similar in character to the small spheroidal particles which appear upon the contents of the germinal vesicle during the latest stages of its existence.

Putting all these circumstances together, I venture to express the belief that this membrane, which the further progress of development proves to be the blastoderm out of which all the parts of this embryo take their rise, results from the metamorphosis of the contents of the germinal vesicle; and that the curved contour which lies towards the upper end of the duct is, in fact, the contour of that side of the germinal vesicle which first becomes filled with the yellow deposit.

Thus far, I feel little difficulty in interpreting the appearances presented; but if the surface and the immediate edges of the blastoderm are examined with great care, minute rod-like bodies will be seen scattered about, so similar in form and size to the heads of the spermatozoa, that I have been frequently tempted to regard them as such, and the more so, as in this stage the duct looks shrunken and shrivelled, and contains but very few, if any, remains of the plug of spermatozoa so conspicuous previously.

In this stage, each of the blastoderms which I have examined has presented these appearances; but as, in spite of long search, the total number which I have found in this state does not exceed four, I do not feel myself in a condition to pronounce positively upon the nature of the bodies in question.

Seventh Stage. *Ovisacs from $\frac{1}{36}$th to $\frac{1}{25}$th of an inch in diameter, in which the blastoderm rapidly increases, and becomes segmented into the rudiments of five zooids.*

Up to this stage the ovisac lies within the sinus system of the parent, which, as I have already pointed out, becomes accommodated to its increased dimensions, partly by the thrusting of the atrial tunic into the cavity of the atrium, but, to a much greater extent, by the formation of a chamber in the test, in consequence of the extension outwards of a diverticulum of the outer tunic. In the recent condition, the blood of the parent must circulate in the narrow space left between the walls of the ovisac and those of its containing chamber; and it seems reasonable to suppose that the former imbibes into its interior a supply of nutritive material, which will contribute towards the subsequent development of the embryo.

But during and after this stage, the ovisac bearing the embryo is to be found loose in the mid-atrium, which, in its later stages, it fills. To arrive at this position it must necessarily break through the wall of the atrium or atrial tunic, and through the duct which still connects it with that tunic. The latter process is easily intelligible, considering the very small relative size and delicacy of the duct; but I confess I do not understand how the rupture of the atrial tunic can be effected without serious hæmorrhage. However, the zooids in which the detached ovisacs have attained a large size appear to be in as good condition as any of the rest.

Henceforward I shall speak of this complex body, composed of the ovisac and the embryo proper, as the *fœtus*, reserving the term *embryo* for the blastoderm and the results of its modification. In such a fœtus as that represented in fig. 10, the blastoderm is a broad, elongated, membranous patch $\frac{1}{63}$rd of an inch long by $\frac{1}{108}$th of an inch wide, and so opaque as at once to strike the eye when the fœtus is viewed with even a very low power. It is composed of somewhat coarse, granular-looking corpuscles, and lies between the membrana propria and the modified epithelium; but the former is separated from it by a very thin layer of structureless substance which extends for some little distance beyond the limits of the blastoderm on each side. The further course of development shows that this layer is the rudiment of the test of the future ascidiarium.

Fœtuses of very slightly increased or even of less size exhibit a marked change in the embryo, which has elongated sufficiently to extend over half the circumference of the ovisac and has, at the same time, become indented at opposite points of its margins, so as to be

marked out into five short segments. One of the two terminal segments becomes much enlarged, spreading over and investing one pole of the ovisac like a cup; while the other four remain far smaller, and, the indentations between them deepening, they are eventually connected only by narrow isthmuses of blastoderm. These segments are the rudiments of as many zooids; but the large cup-like one has a totally different fate from the rest, and for distinction's sake I shall term it the *cyathozooid*, while the others are, in their order of nearness to it, the 1st, 2nd, 3rd, and 4th ascidiozooids[1] respectively. The zooids are not merely connected with one another by the isthmuses of blastoderm above-mentioned, but the structureless test has greatly increased in thickness, and now invests them all, like a thick layer of transparent varnish. The membrana propria of the ovisac is no longer distinguishable outside this rudimentary test.

The remains of the duct are often still traceable, towards the conclusion of this stage, at one end of an equatorial diameter of the fœtus (supposing the cyathozooid to be situated at one of its poles); but later, it is no longer to be discovered.

Eighth Stage. *Fœtuses from $\frac{1}{25}$th of an inch up to the largest which have been met with.*

In describing this final stage of development, it will be convenient to consider, first, the changes in general arrangement, size and form, of the different parts of the fœtus; and secondly, the special modifications which each of these parts undergoes.

The cyathozooid, at first, occupies but a comparatively small segment of the surface of the spheroidal fœtus, and the slightly curved series of ascidiozooids stretches out from it, over about half the circumference of the uncovered portion of the ovisac (Pl. XXXI. [Plate 30] fig. 11). But, by degrees, the cyathozooid extends so far as to invest nearly half the surface of the ovisac, and, at the same time, the chain of ascidiozooids (considered as a whole) gradually assumes a new direction, and applies itself closely to the face of the cyathozooid, whose circumference it half encircles (fig. 13). The blastoderm of the ascidiozooids, however, remains perfectly distinct from that of the cyathozooid, the two being united only by the layer of test, which, in the earlier stages, invested both, and whose contiguous edges now seem to run into one another.

[1] I have, throughout the present memoir, used the term 'ascidiozooid,' as more euphonious than 'ascidiite,' employed in my notice in the 'Annals of Natural History' for 1860.

If a line traversing the centre of the cyathozooid and the centre of the ovisac be regarded as the axis of the whole fœtus, then, in the present condition, the longest diameters of the first and of the last ascidiozooids are parallel with that axis, and that extremity of each, at which the elæoblast is situated, is directed away from the cyathozooid. The long diameters of the intermediate ascidiozooids, on the other hand, cut the axis of the fœtus at a high angle, their elæoblastic ends being those which are nearer the cyathozooid (fig. 13).

As development advances, the first and the fourth ascidiozooids retain their parallelism to the axis of the fœtus, while the whole series elongates, so that the fourth comes to be situated close to the first (Plate XXXI. [Plate 30] fig. 14), the four encircling the base of the cyathozooid completely. This elongation of the whole series is effected, mainly, at the expense of the isthmuses, which elongate so much as to be converted into slender cords, of which the first connects the cyathozooid with the neural face of the first ascidiozooid; the second connects the hæmal region of the first ascidiozooid, at a point just opposite the endostylic cone, with the neural face of the second ascidiozooid; the third similarly unites the second and the third; and the fourth, the third and fourth.

But the elongation of the isthmuses is not merely sufficient to allow the fourth ascidiozooid to come close to the third; it is also enough to permit of a movement of rotation on the part of the second and third ascidiozooids. The first and fourth, as has been seen, early take up such a position that their long axes are parallel with the axis of the fœtus; and, by degrees, the second and third revolve, their adjacent ends being allowed to separate by the elongation of their connecting isthmuses, until their long diameters, from being very obliquely inclined to that axis, also become parallel with it, and with the long diameter of the first and fourth. Thus, at last, the long diameters of all four ascidiozooids are parallel with one another and with the axis of the fœtus, their similar ends being turned the same way (fig. 14), while the isthmuses slope obliquely from the neural region of one to the hæmal region of the next. The long diameter of each ascidiozooid is at right angles with its proper axis (which would be a line drawn from the oral to the cloacal aperture), and, hence, the neural and hæmal sides of the body are at opposite ends of its long diameter. The neural side is that which is turned in the same direction as the aperture of the cyathozooid, while the hæmal side is the opposite. The mouth is at that end of the true axis or short diameter of the body which is turned outwards; while the atrial aperture eventually makes its appearance at the other

end of this diameter and, consequently, on that face of the ascidiozooid which is adjacent to the ovisac and cyathozooid.

At the commencement of the series of changes here indicated the ascidiozooids are, individually, much smaller than the combined cyathozooid and ovisac; but as development advances, the latter diminish while the former increase; and as, by the increase of size of the ascidiozooids, the interval between them becomes both relatively and absolutely less, they, at last, completely hide the combined cyathozooid and ovisac from view, so that it is not always an easy matter to find the latter (Plate XXXI. [Plate 30] fig. 15). The test increases, concomitantly with the ascidiozooids, enveloping them and filling up their intervals so as, finally, to form a spheroidal investment for the entire tetrazooidal fœtus (figs. 14 & 15).

During the whole of these changes and until the fœtus attains a diameter of $\frac{1}{14}$th of an inch, it remains within the mid-atrium of the parent, which, at last, it completely fills. With Savigny, I am unable to understand how it escapes, unless indeed it becomes freed by the destruction of its parent. For it seems quite impossible that the fœtus should find a way open to it by any conceivable amount of dilatation of the atrial aperture. Nor does one ever find a fully formed ascidiozooid without a fœtus in its mid-atrium. And if, at the same time, it is recollected that only one ovum ever comes to maturity in an ascidiozooid, so that when the fœtus has arrived at its full development the parent's "occupation is gone," it seems less improbable that the destruction of the latter should be involved in the maturity of its offspring.

Such is a general description of the changes in the size, form, and position of the chief constituents of the fœtus, in virtue of which it assumes its final characters. It now becomes necessary to trace the internal modifications which each of these constituents undergoes.

1. *The Cyathozooid.*—In my brief preliminary sketch of the development of *Pyrosoma* ('Annals of Natural History' for January, 1860), I have termed this part the "rudimentary cloaca;" but it would have been a more accurate account of the matter, if I had called it the 'mould' or 'forerunner' of the cloaca. Rudiment of the cloaca, in the strict sense of the words, it is not; for, as we shall see, the atrial apertures of the ascidiozooids never really open into it.

When the cyathozooid is first distinguishable as a separate segment and traces of structure are discernible in it (Plate XXXI. [Plate 30] fig. 11), it presents, when viewed from above, near that edge which is most distant from the first isthmus, a rounded depression. Viewed sideways, the blastoderm appears to be divided into

two lamellæ, the separation between which is most marked immediately under the depression. In a line between the depression and the first isthmus a clear streak is visible, the first rudiment of what I shall term the *appendix of the cyathozooid.* As the development of the fœtus progresses, the interspace between the two layers of the blastoderm enlarges and the depression becomes an opening, into which, however, the thick test is continued, projecting like a conical tongue into the interspace or cavity just mentioned, in such a manner as to leave but a narrow median passage, by which I conceive that a free communication between the cavity of the cyathozooid and the exterior must be effected (figs. 17 & 18). At the same time, the aperture is gradually shifted from the margin to the centre of the cyathozooid, so that, eventually, its middle corresponds to one pole of the fœtus (fig. 14), and gives the latter the appearance of a cup, or of an egg with its top cut off. Contemporaneously with these changes that streak which I have mentioned takes shape as a singular appendage situated between the two layers into which the outer wall of the cyathozooid is differentiated, and a communication, which, I believe, existed from the first between the cyathozooid and the first ascidiozooid by means of the first isthmus, becomes patent and obvious. But a description of the structure of a more advanced cyathozooid will best render these changes intelligible.

Fig. 14 represents a fœtus $\frac{1}{18}$th of an inch in diameter. The cyathozooid and ovisac, taken together, have the form of an ellipsoid, truncated at that end which presents the aperture of the cyathozooid, and rounded at the other. The circular aperture of the cyathozooid (β) is $\frac{1}{105}$th of an inch across, and is bounded by a constricted perpendicular lip $\frac{1}{400}$th of an inch deep. The aperture leads into a wide cavity about as deep as the lip (γ), into which the prolonged tongue of the test projects. The canal which traverses the centre of this tongue, and which consequently must place the cavity of the cyathozooid in communication with the exterior, appears very distinct. The appendix (δ) has the form of a curved tube, with its concavity turned towards the cavity of the cyathozooid. Its anterior end is slightly enlarged, while its posterior end, also a little dilated, is seated upon a slight prominence: both ends seem to be open.

On one side of this appendix, a canal (θ), $\frac{1}{150}$th of an inch long by $\frac{1}{950}$th wide, passes obliquely towards the cavity of the cyathozooid and apparently opens into it. Posteriorly it is continued, at an obtuse angle, into a similar tube having about the same length, and eventually passing into the first isthmus, now $\frac{1}{126}$th of an inch long. It will be observed that, notwithstanding the advanced condition of

the ascidiozooids in this fœtus, their upper extremities do not rise so high as the level of the middle of the ellipsoid formed by the cyathozooid and ovisac. The point at which their atrial apertures will eventually be formed, consequently, can hardly be so high as the lower end of that ellipsoid.

As has been already hinted, with the advance of the fœtuses in size all their relations become changed. The ascidiozooids, instead of presenting a fraction of the length of the combined ellipsoidal cyathozooid and ovisac, and occupying only a small portion of the mass of the fœtal spheroid, gradually become fully thrice as high as the ellipsoid in question, and form by far the greater proportion of the mass of the spheroid (fig. 15). The ovisac and cyathozooid, again, diminish, not only relatively but absolutely (fig. 16), inasmuch as their largest diameter does not eventually amount to more than $\frac{1}{70}$th or $\frac{1}{80}$th of an inch, while the lip and the internal cavity of the cyathozooid become less distinct structures than before.

But the most curious change is that which has taken place in the test in the vicinity of the cyathozooid. It has, as it were, separated itself from the latter, following the ascidiozooids as their vertical diameter increases, whereby the central tongue of the test is pulled completely out of the mouth of the cyathozooid, as one might pull a finger out of a glove (compare figs. 18 and 19, Plate XXXI.) [Plate 30]. As a consequence of this operation a cavity, which gradually increases in dimensions, is developed between the outer surface of the cyathozooid and the inner wall of the test; and as the atrial ends of the ascidiozooids ascend in consequence of the growth of the latter, they open into this cavity, which thus manifests itself as the cloaca (fig. 19). The tongue-like prolongation of the test becoming pulled out and flattened as the cloaca widens, ultimately ceases to project into the cavity of the latter, and becomes converted into the lip of its aperture. In fig. 19 it still protrudes for some distance into the cloacal cavity.

2. *The Ascidiozooids.*—From their small size, flattened form and general opacity, it is by no means so easy to trace satisfactorily the successive changes by which the other segments of the blastoderm are converted into perfect ascidiozooids, as it is to follow out the development of the buds. Nevertheless, knowing the latter process, it is not difficult to interpret the appearances presented by the segments of the blastoderm, in the course of their development.

When the blastoderm first becomes marked out into those segments which eventually constitute the ascidiozooids (Plate XXXI. [Plate 30] figs. 11 and 12), each segment is about $\frac{1}{126}$th of an inch

long by as much broad, and has a thickness of less than $\frac{1}{500}$th of an inch. Like the blastoderm whence it proceeded, the segment appears to consist of nothing but a dense, opaque mass of indifferent tissue.

In a somewhat more advanced condition, the first signs of organization appear in the form of a clear median longitudinal streak visible in each segment when it is viewed from above. The streak is bounded by two more-opaque lines, and on each side of the whole is a more opaque mass. If the fœtus be turned, so as to display a transverse section of one of the segments, the clear streak is seen to correspond with a central cavity answering to the alimentary tract of a bud, while the more opaque lateral masses are plainly small sacs—the lateral atria. The isthmus between any one segment and the next is clear in the middle, and has every appearance of a tube connecting the alimentary tracts of the two segments ; but if, as I have already said, the first isthmus enables the alimentary tract of the first ascidiozooid to communicate with the cavity of the cyathozooid, then the cavities of all the alimentary tracts of the ascidiozooids must be, indirectly, in communication with this cavity and, through it, with the exterior. In point of fact, I believe that the four primary ascidiozooids stand in the same relation to the cyathozooid, as four buds formed from the ascidiozooids in the way described above would do, if, in the process of gemmation as many remained connected together and with the parent; for, as we have seen, all the branchial sacs of the buds communicate with that of the parent and, by the latter, with the exterior. And the mode of connexion of the different ascidiozooids is exactly the same in the two cases ; for, in somewhat more advanced fœtuses (in which the ascidiozooids are about $\frac{1}{100}$th of an inch long and broad), it is obvious that the clear streak above mentioned corresponds with the interval between the bands of the endostyle, and that the end of the alimentary tract of any one embryonic ascidiozooid which is continued into the isthmus corresponds with the endostylic cone of ordinary buds; while that part of any embryonic ascidiozooid which receives an isthmus is the interval between the œsophageal aperture and the ganglion, just as this is the place into which the peduncle of a bud opens.

In ascidiozooids of this size, the nature of what I have termed the lateral atria is demonstrated by the appearance of four or five stigmata in their inner wall, just as in buds at a corresponding stage. At the same time, that part of the indifferent tissue of the embryo which lies in the immediate vicinity of the pointed end of the alimentary tract (the future endostylic cone) becomes converted into a mass of clear reticulated tissue, the elæoblast (*æ*). This body is

developed more largely laterally than in the middle line, so that it appears, at first, as if it were composed of two distinct portions; but its two moieties are really continuous with one another on the hæmal side of the alimentary tract. The position of the future oral aperture is just indicated in the middle of the exposed surface of the ascidiozooids in this stage; but I could not ascertain anything definite as to the condition of the intestine. Indeed, from the flattened form of the embryonic ascidiozooids and their close apposition to the ovisac, it is exceedingly difficult to decipher all the details of their internal structure.

Ascidiozooids of $\frac{1}{70}$th of an inch in length exhibit a well-defined, though not open oral aperture, $\frac{1}{380}$th of an inch in diameter. The branchial stigmata have increased in number to nine or ten on each side and the middle ones occupy the whole depth of the branchial sac; but there are, as yet, no longitudinal branchial bars. The mode of origin of the stigmata appears to be just the same as in the buds.

The nervous ganglion makes its appearance as a thick mass of indifferent tissue between the isthmus and the oral aperture; and the contour of the gastro-intestinal part of the alimentary canal is discernible on that face of the embryo which is nearest the ovisac. The isthmuses have lengthened to $\frac{1}{380}$th of an inch.

A fœtus $\frac{1}{24}$th of an inch long, whose ascidiozooids had a length of $\frac{1}{63}$rd of an inch, presented the clear profile view of one of the latter, which is represented in Pl. XXXI. [Plate 30] fig. 13*a*. The central tube or canal of the first isthmus is obvious, and it opens freely into the branchial sac of the ascidiozooid between the ganglion and the oral aperture. The central canal in question is bounded by the inner tunic of the ascidiozooid, between which and the outer tunic is an interval which is connected, on the one hand, with the sinuses of the ascidiozooid, and on the other, with the space between the two walls of the cyathozooid. The ganglion is very distinct and occupies nearly the whole interval between the oral aperture and the isthmus.

The diapharyngeal band, already visible in earlier stages, is continued from above the posterior half of the ganglion to the roof of the branchial cavity; but its proportions are more slender, as it measures $\frac{1}{240}$th of an inch long, by $\frac{1}{1920}$th of an inch thick. The oral aperture is not open, but its lobed tentacular fringe may be observed, the hæmal tentacle being even now distinguished from the rest of the fringe by its length and form.

Nine or ten branchial stigmata are discernible; but there are, as yet, no longitudinal branchial bars. The intestine is completely

fashioned; and the elæoblast is large, conspicuous, and composed of a reticulated tissue.

In a fœtus $\frac{1}{21}$st of an inch long, with ascidiozooids $\frac{1}{56}$th of an inch long by $\frac{1}{64}$th of an inch from their oral to their cloacal extremities and nearly hemispherical in form (the flat side of the hemisphere being applied to the combined ovisac and cyathozooid), the isthmuses measure $\frac{1}{250}$th of an inch in length; and it is obvious that, while their central canals connect together the branchial sacs, the interspaces between their double walls place the sinuses of the ascidiozooids in communication. There are ten branchial stigmata, of which the first and last are very small; and six or seven longitudinal branchial bars have made their appearance. The mid-atrium is distinctly developed below and behind the gastro-œsophageal part of the alimentary canal. The place of the atrial aperture is indicated by the union of the atrial and outer tunics, in a round spot at the posterior part of the mid-atrium. In fact, the whole zooid is nearly in the same condition as the bud represented in Pl. XXX. [Plate 29] fig. 22. The renal (?) organ has made its appearance as a patch of opaque yellowish cells.

Ascidiozooids $\frac{1}{42}$nd of an inch long, by $\frac{1}{56}$th from their oral to their cloacal apertures, which form part of a fœtus $\frac{1}{18}$th of an inch long, and surround the lower half of the combined cyathozooid and ovisac, have ten or eleven stigmata and seven longitudinal branchial bars. The hæmal tentacle is well developed, the rudiment of the ciliated sac is discernible, and between the aperture of the central canal of the isthmus and the œsophagus are two rudimentary languets. The diapharyngeal band is very slender. The elæoblast has a length of about $\frac{1}{90}$th of an inch. The rudiment of the atrial aperture (round, and about $\frac{1}{330}$th of an inch in diameter) lies altogether below the level of the equator of the combined cyathozooid and ovisac. There is an indistinct appearance as of a small cavity between it and the latter organs. The posterior end of the endostyle appears quite distinctly to be continued back into the central canal of the isthmus. The rudiment of the heart is obvious, in close connexion with, and apparently developed from the wall of the branchial sac; and there are two slight papillary elevations in the place whence the stolons will be given off.

In a fœtus of about the same diameter as the preceding but whose ascidiozooids have a vertical diameter of $\frac{1}{33}$rd of an inch, while the combined cyathozooid and ovisac are $\frac{1}{50}$th of an inch long, the neural boundaries of the ascidiozooids project a little way beyond the open end of the cyathozooid. The upper edges of their atrial

apertures, now $\frac{1}{180}$th of an inch in diameter, are still fully $\frac{1}{210}$th of an inch below the margin of the cyathozooid; and although the formation of the true cloacal chamber has commenced by the separation of the test from its cyathozooidal mould, yet its depth is so slight (not more than $\frac{1}{530}$th of an inch) that the end of the tongue-like inward prolongation of the test still lies between the lips of the mouth of the cyathozooid.

A fœtus of $\frac{1}{16}$th of an inch in diameter has the combined cyathozooid and ovisac not more than $\frac{1}{36}$th of an inch long, and cup-shaped—its upper, open end being as broad as its middle. The atrial apertures of the ascidiozooids (which measure $\frac{1}{30}$th of an inch in long diameter) are vertically oval, $\frac{1}{80}$th of an inch long, and lie almost wholly above the level of the upper edge of the cyathozooid. They open at once into the cloacal cavity, which, as measured from its roof, formed by the now hardly-projecting tongue-shaped process, to the upper edge of the cyathozooid, is $\frac{1}{84}$th of an inch deep.

The stolons of this fœtus are $\frac{1}{336}$th of an inch long, and are directed towards the aperture of the cloaca.

In one of the most advanced fœtuses I have met with (Pl. XXXI. [Plate 30] fig. 15), about $\frac{1}{15}$th of an inch in diameter, the greatest length of the ascidiozooids (or the diameter parallel to the fœtal axis) was $\frac{1}{22}$nd of an inch, while their antero-posterior diameter was $\frac{1}{42}$nd of an inch. The long diameter of the combined ovisac and cyathozooid (the latter being now completely hidden between the hæmal moieties of the ascidiozooids) was only $\frac{1}{76}$th of an inch; or, in other words, they had not a third of their former dimensions. Each ascidiozooid of this fœtus has a roughly semicircular profile, the straight side being turned towards the axis of the fœtus. The curved contour is more convex on the hæmal, more flattened upon the neural face. From side to side each ascidiozooid is much compressed, so as not to measure more than $\frac{1}{56}$th of an inch in this direction.

The oral aperture is not yet pervious; but a circular groove of the outer surface of the test, $\frac{1}{95}$th of an inch in diameter, indicates the area in whose centre it will appear, around which centre lie the oral sphincter and the tentacular fringe. The latter, at present, not only projects into the buccal cavity but is divided into its processes; and the hæmal tentacle, $\frac{1}{316}$th of an inch long, exhibits its characteristic enlarged base and finger-like process. The peripharyngeal ridge exhibits its distinctive structure. Rather in front of its upper loop, a small process (the upper end of the diapharyngeal band) projects from the roof of the pharyngeal sac; and a corresponding remnant of the lower end of the same band is seen, as a small projection of

the neural wall of the cavity, just above the tubercle of the ganglion.

The urinary (?) organ is very distinct as a mass of pale, spheroidal granular bodies, and occupies its normal place.

The ganglion, and so much as could be made out of the ciliated sac are similar to the same structures in adults ; but the ganglion has a length of only $\frac{1}{240}$th of an inch.

In one of the ascidiozooids of this specimen the isthmus can be well studied as it passes off from the neural side immediately behind the ganglion. Where it joins the ascidiozooid it is $\frac{1}{275}$th of an inch wide, but, in the middle of its length, it has a diameter of not more than $\frac{1}{870}$th of an inch. In consequence of its passing obliquely from the neural face of one ascidiozooid to the hæmal face of the next, it is, of course, rather longer than the largest diameter of the ascidiozooid (or more than $\frac{1}{22}$nd of an inch long). Viewed from the side, it looks like a clear, transparent tube, divided by a partition into two channels ; but where it bends round, and so exhibits a transverse section, this partition is itself clearly seen not to be a simple septum, but to be formed by two membranous lamellæ, which stretch from wall to wall of the isthmus, and are themselves separated by an interval of $\frac{1}{4800}$th of an inch. In fact, the central canal has now assumed this partition-like character. If traced up to the neural wall of the one ascidiozooid with which it is connected, the outer membrane of the isthmus obviously passes into the outer tunic of the ascidiozooid, while the walls of its contained, inner canal are continuous with the inner tunic, or pharyngeal mucous membrane, of the same part. On the other hand, if it be followed to the hæmal wall of the other ascidiozooid, the outer membrane of the isthmus passes into the outer tunic of that region, while the wall of the inner tube is continuous with the endostylic cone. It is obvious, therefore, that the composition of the isthmus is, in reality, the same as in earlier stages and that, while its central canal connects the pharyngeal cavities of the two ascidiozooids, the interspace between this canal and the outer walls of the isthmus connects their sinuses.

Between the attachment of the isthmus and the œsophageal aperture only two languets are developed from the hypopharyngeal region. The great sinus beneath them is full of agglomerated blood-corpuscles.

The endostyle is still broad proportionally ($\frac{1}{150}$th of an inch), but all its parts are well developed. It ends posteriorly in a short process or endostylic cone, $\frac{1}{380}$th of an inch long, which, as I have said above, passes into the central tube of the isthmus.

A cellular mass, $\frac{1}{510}$th of an inch long, is attached to the external tunic, close to the end of the endostylic cone, if not directly connected with it ; and this, I am inclined to think, is the rudiment of the generative blastema. I have not been able to detect any distinct structure (as of an ovisac or testis) in it, which is remarkable when one considers the early appearance of the ovisac in the buds.

The branchial stigmata are altogether twelve in number. The anterior and posterior are rudimentary while most of the others extend across almost the whole depth of the branchial sac. The cilia are perfectly distinct upon their edges. The longitudinal branchial bars are nine in number. The intestine has nearly the same form as in the adult, and the tubular, hepatic system is well formed. The heart is visible in its place. The elæoblast is a mass of clear reticulated tissue, causing the hæmal wall to bulge a little on each side of the middle line, and occupying the interval between the endostyle and generative blastema, on the one hand, and the heart and intestine on the other.

The atrial aperture is enormous in proportion, occupying the greater part of the inner face of the ascidiozooid above the level of the cyathozooid and attaining a length of fully $\frac{1}{42}$nd of an inch and a breadth of $\frac{1}{112}$th of an inch. In other words, the atrial aperture is six times as large as it is in the adult ascidiozooid, though the latter is at least eight or ten times as large as one of the zooids of the fœtus under description. In consequence of the great proportional size of these oval apertures, whose long diameters are parallel with the axes of the fœtus, the intervening wall of the cloaca is very narrow.

The cyathozooid and ovisac are $\frac{1}{50}$th of an inch long by $\frac{1}{70}$th wide and more cylindrical than cup-shaped. The aperture, still distinctly visible, has a diameter of $\frac{1}{500}$th of an inch ; and as the cloacal chamber is now $\frac{1}{34}$th of an inch deep, the margin of the aperture is but just on a level with the convex, neural margin of the œsophagus of any of the ascidiozooids. Where the former tongue-like process existed, the roof of the cloaca now hardly projects inwards at all.

The atrial muscles are visible as very delicate, straight bands, $\frac{1}{17}$th of an inch long by $\frac{1}{3400}$th wide, which take an oblique course on each side, from a point a little below the end of the endostyle, neurad and a little forwards, to a point opposite the commencement of the œsophagus. In the middle of their course these bands lie very near the lips of the atrial aperture.

The stolons are $\frac{1}{230}$th of an inch long; they pass almost horizontally inwards, towards the rudimentary lip of the cloaca, and are curved towards its cavity, at their blind extremities. The corpuscles of which their walls are composed are more elongated than before and, sending processes into the adjacent substance of the test, cause the cæcal ends of the stolons to have a very peculiar, brushlike appearance.

3. *The Test.*—As I propose to reserve the description of the histological changes undergone by the embryo of *Pyrosoma* for another occasion, I will merely state, in this place, that the test appears, at first, to be a structureless excretion. Subsequently, cellular bodies, like connective-tissue corpuscles, are discernible in its most superficial layer, and are disposed in such a manner as to form a very regular, hexagonal network, with large meshes. The most advanced fœtus has presented neither of the fibrous layers visible in the adult test.

Ninth Stage. *The conversion of the tetrazooidal fœtus into the adult ascidiarium.*

The most advanced fœtus which has been described differs from the adult ascidiarium not merely in size, in the paucity of its ascidiozooids, in the form and proportions of the latter, in the absence of buds, or ever so slightly differentiated reproductive organs, in them, and in their large atrial apertures (all of which are peculiarities which we may easily conceive to be altered by age and growth), but in still more important characters, seeing that in the adult ascidiarium I have met with no trace of the cyathozooid or the isthmuses, nor have I been able to discover any ascidiozooid with two stolons.

The first theory of the mode of formation of the adult ascidiarium which suggests itself is obviously that which supposes that the four ascidiozooids of the fœtus give rise, by budding, to all those of the adult *Pyrosoma*, at the same time losing the two stolons, and acquiring reproductive organs, so as to be undistinguishable from their agamogenetic progeny.

But difficulties arise when we compare this theoretical conception with the structural characters, and the ascertained laws of gemmation of *Pyrosoma*.

In every ascidiozooid of the adult ascidiarium (and there is no reason to suppose that those of the tetrazooidal fœtus constitute exceptions to the rule) budding takes place, as we have seen, from a single definite region of the body, situated in the posterior moiety

of the hæmal surface; and the buds remain, in nearly the same plane as that in which they were given off, until they have attained some distance from the parent. It has been seen, in fact, that three buds given off successively from one ascidiozooid, may be visible, one below the other, in the same, not very thick, longitudinal section. But in the tetrazooid, as in the adult, the hæmal side is that turned away from the aperture of the ascidiarium. If, then, the buds thrown off from the ascidiozooids of the fœtus all remain on the hæmal, or apical, side of their parents, we ought, on examining the adult organism, to find the four primitive ascidiozooids close to the margin, with a series of two or three buds, in various stages of development, attached to each.

As a matter of fact, however, no section taken near the margin of the aperture has ever presented an appearance essentially different from that represented in Pl. XXX. [Plate 29] fig. 4. The ascidiozooids have always been young, and, on the average, younger, the nearer they were to the margin. But they have never been younger than such a bud as is represented in fig. 24, Pl. XXX. [Plate 29]; and those of the first three or four tiers have always possessed imperfectly developed sexual organs, and buds not more advanced than those represented in figs. 19 and 20.

That the ascidiozooids which lie nearest the aperture are the result of the budding of other ascidiozooids is beyond all doubt. As I have traced the development of the stolon from such a modified bud, it is clear that the bud is not developed, as I had once imagined, from the stolon of another ascidiozooid,—these stolons being invariably traceable, without a break, into the lip of the cloaca, where they end cæcally. There appears to me, then, to be no other course open but to suppose that these young ascidiozooids which lie nearest the aperture, are buds which were originally developed from the hæmal region of ascidiozooids which lie nearer the apex, and that they have consequently passed round and to the neural side of their parents. If this migration of the buds really occurs, it will follow, as Savigny supposed, that the four apical ascidiozooids of the adult are the modified zooids of the fœtus,—the buds developed from their hæmal walls not remaining upon their apical side, but passing up between them on to their neural sides, and there becoming themselves new centres, whence fresh buds are thrown off, which gradually take their places in a still higher tier.

I can conceive of no other mode in which the structure of the fœtus, the structure of the adult and the law of budding can be reconciled; and yet I am reluctant to admit so seemingly artificial a

process on anything short of direct evidence. Such evidence, however, is only to be obtained by the examination of young *Pyrosomata* but little larger than fœtuses, none of which have come into my possession.

§ 5. *Summary and discussion of the results of the observations on the gamogenetic development of* PYROSOMA GIGANTEUM.

If the observations detailed in the preceding pages be correct, and no flaw be found in that interpretation of them which has been offered, it follows that—

1. The ovisac of *Pyrosoma* at first contains an ovum, altogether similar to that of other animals, and in particular resembling that of many *Cœlenterata*, *Molluscoida*, and *Mollusca*, in the absence of a vitelline membrane.

2. Impregnation is effected by the passage of the spermatozoa up the duct of the ovisac, and it would seem that these spermatozoa must immediately come into contact with the yelk; but when, and how, the essential act of fecundation (consisting in the action of the spermatozoa upon the germ) takes place, does not appear.

3. There is neither complete nor partial, yelk-division; but the vitellus disappears, as such, apparently becoming diffused through the contents of the ovisac, which rapidly increases in size. By this deliquescence of the yelk the germinal vesicle is laid bare.

4. The germinal vesicle adheres to a particular spot of the epithelial lining of the ovisac, close to the opening of its duct and, eventually traversing that epithelial lining, takes up a position between it and the *membrana propria* of the ovisac.

5. In the meanwhile, a turbid deposit takes place in that moiety of the germinal vesicle which lies nearest the aperture of the duct; and the germinal spot, a remarkably obvious structure in this and preceding stages, is partially imbedded in this deposit.

6. The germinal vesicle grows and becomes more flattened; but soon, although it is quite translucent, the germinal spot can no longer be found in it. In the place of that structure and resulting, as I suppose, from its division, a number of small, clear, spheroidal corpuscles are visible upon the face of the deposit in the germinal vesicle.

7. Next, the germinal vesicle, as such, is no longer visible; but, occupying the same place, preserving the same colour, having very nearly the same size and, on the side turned towards the duct, the same curved contour, there is a flat patch, consisting of a single layer

of excessively delicate corpuscles, each with its clear space and central particle—constituting the commencement of the blastoderm.

8. The blastoderm enlarges, assumes a band-like form, and becomes divided by constrictions into five segments: of these, one becomes the cyathozooid—a temporary structure, which is especially attached to one pole of the ovisac, and, among other purposes, serves as a sort of precursor, or mould, of the cloaca; the other four are converted into ascidiozooids.

9. The ascidiozooids enlarge and eventually give rise to the tetrazooidal fœtus described by Savigny. The cyathozooid and the ovisac which it surmounts diminish in size and, probably, eventually disappear. The lining epithelium of the ovisac early acquires a peculiar vesicular structure.

10. All these changes, subsequent to the formation of the blastoderm, take place in the mid-atrium of the parent, which the fœtus, at length, completely fills. There appears to be no placental connexion between the fœtus and the parent; but the nutritive matter contained in the large ovisac may well be supposed to pass into the sinuses of the cyathozooid and thence into those of the ascídiozooid, and thus to subserve the nutrition of the whole fœtus.

In successively commenting upon the preceding paragraphs, I shall consider how far the embryogeny of *Pyrosoma* can be parallelled by that of other animals, and how far it offers exceptional peculiarities.

1. I do not think that any one, acquainted with the structure of the ovarian ova of other Ascidians and of the *Mollusca* generally, will entertain the slightest doubt that the parts called germinal spot, germ nal vesicle and vitellus, respectively, in the preceding pages, really have the nature I have assigned to them. The ovisac corresponds with a single acinus of the ovary of other *Mollusca* and *Molluscoida*, and is altogether similar to the solitary ovisac of *Salpa*.

2. The process of impregnation presents nothing anomalous; but, as regards the act of fecundation, it is remarkable that the spermatozoa should so long remain aggregated in a mass in the upper end of the duct, without, to all appearance, penetrating into the cavity of the ovisac or into the substance of the yelk. Still more singular is that appearance of scattered, rod-like bodies, not unlike the heads of spermatozoa, upon and about the very young blastoderm. If I could feel thoroughly assured that these bodies are really the spermatozoa, I should be inclined to follow out to some length a series of considerations suggested by the fact, as to the essential nature and place of occurrence of impregnation. For the present, however, I will merely remind the reader that the so-called 'disappearance of the

germinal vesicle,' and even a certain progress in yelk-division, may take place without impregnation;[1] whence it may seem less strange than it appears at first sight, to suppose that the influence of the spermatozoa may be exerted, in some cases, not upon the yelk, nor upon the germinal vesicle as such, but upon the nascent blastoderm.

3. The only animals which, so far as I know, present a condition of the yelk at all comparable to its liquefied and pellucid state in *Pyrosoma*, are *Ascaris dentata*, *Cucullanus elegans*, and *Oxyuris ambigua*. In these nematoid worms, the vitellus, according to Kölliker[2], is represented only by a clear, transparent fluid containing a very few granules, and it takes no direct share whatever in the formation of the embryo. The vitellus seems to play an equally subordinate part in the great majority of the *Articulata*, but in these animals it is commonly opaque and granular.

4. If the ovisac of *Pyrosoma* be compared with the Graafian follicle of a mammal, the resemblance (notwithstanding their obvious differences) of the two structures is marked; and the manner in which the germinal vesicle traverses the epithelium of the ovisac of *Pyrosoma* is singularly like the manner in which the mammalian ovum imbeds itself among the cells of the proligerous disk. A still closer parallel, perhaps, is presented by the bird's egg, if we consider the mode in which its germinal vesicle (which at first occupies the centre of the future egg, and is contained in a primitive ovum surrounded by, at any rate, a rudimentary vitelline membrane) passes to the surface, and eventually lies immediately beneath the membrane which encloses the food-yelk[3].

5, 6, 7. The consideration of the phenomena enumerated under these heads opens up the whole vexed question of the fate of the germinal vesicle.

Since the imaginations of Dr. Martin Barry have fallen into just discredit, most physiologists have more or less distinctly adopted the doctrine that the germinal vesicle and its contents lose their identity and disappear; and that the embryo-cells, whence the blastoderm arises, are new structures not directly derived from them.

[1] See Leuckart, art. "Zeugung," Wagner's Handwörterbuch, iv. p. 958. What Leuckart says here about the Frog is not in accordance with the results of the careful experiments of Newport (Phil. Trans. 1851, p. 190), who arrives at the conclusion that segmentation certainly does not take place in the unimpregnated ovum. Vogt's case is not satisfactory, as there is no counter evidence to show that impregnated ova would have developed under the circumstances. Bischoff's observations on the Sow (Ann. des Sci. Nat. 1844), however, appear to be unexceptionable evidence.

[2] Beiträge zur Entwickelungs-geschichte wirbelloser Thiere. Müller's Archiv, 1843.

[3] See Dr. A. Thomson's admirable article "Ovum" in Todd's Cyclopædia.

The evidence by which this conclusion is supported, however, will be found, if closely sifted, to be, for the most part, not only negative, as by the nature of the case it must be, but weakly negative. That is to say, not only is the conclusion based upon the circumstance that, at a given period, the observer was unable to find the germinal vesicle or to identify its contents,—but, in most cases, the circumstances are such that he might very well have missed them had they existed. Even in *Pyrosoma* it is no easy matter, until one has had some practice, to find the germinal vesicle when it is passing into the blastoderm, although, in all the earlier stages, nothing can be more obvious; and had the ovisac of *Pyrosoma* been filled with even a very slightly granular yelk, I believe the discovery of the germinal vesicle, at this period, would be almost impracticable. What wonder, then, that it should be impossible to identify the germinal vesicle or its contents in the midst of the more or less opaque and coarsely granular substance of which the yelk of ninety-nine ova out of a hundred is composed? The only case to which this reasoning does not apply is that described by Kölliker in the paper already referred to (*l. c.* p. 76):—

"As regards the internal changes undergone by the eggs [of *Ascaris dentata*], the most striking fact is that, immediately after fecundation, the germinal spot and the germinal vesicle have disappeared and the clear and transparent yelk contains nothing but scanty elementary granules. This is a point of great importance; and to show that there is no possibility of being deceived about it, I add, that the ovum of *Ascaris dentata*, including its chorion and vitelline membrane, is so transparent that all the outlines of a body which may happen to lie beneath it are quite sharply and distinctly recognizable, and its contents are so clear and patent that hardly the smallest elementary granule of the yelk can remain hidden. Which of the two parts first disappears, the germinal spot or the germinal vesicle, I cannot as yet say with certainty; but, in one individual, I saw two ova which had hardly traversed the seminal cells in the fundus uteri, and though they still exhibited a germinal vesicle, had no germinal spot. In another individual, I observed the same thing in an ovum imbedded in the midst of the seminal cells; so that I have some ground for the opinion that it is the germinal spot which disappears first. Further and repeated observations must decide whether this is the rule or whether, in other cases, it is not the germinal vesicle which disappears first. But I must observe, that this first stage of the development of the ova appears to be of very short duration; for, while no fecundated female *Ascaris* which I

examined would have failed to supply me with a complete series of all the other stages of development, it was but thus rarely that these first processes presented themselves.

"As the ovum, now deprived of its germinal vesicle and spot, is propelled downwards by the peristaltic contractions of the uterus, the first embryo-cell is formed in the middle of its clear yelk. I have never been able to detect the mode of its origin. . . . . By endogenous development, the embryo-cells give rise to other cells, which become the blastodermic mass whence the embryo is formed. The yelk, as such, disappears."

I am prepared to admit the full force of this carefully observed example of the disappearance of the germinal vesicle and the merging of its contents in the yelk, but it is the only case, within my knowledge, to which great weight can be attached; while, on the other hand, independent observers have (of late years) recorded equally definite and positive observations that in some groups of animals, at any rate, the germinal vesicle does not disappear, but that it gives rise by division to the primary cells of the embryo.

Thus, Dr. Nelson, in his memoir "On the Reproduction of *Ascaris mystax*" (Phil. Trans. 1852, pp. 580, 581), affirms that the germinal vesicle of the impregnated egg of this worm bursts, and sets free the germinal spot, which is directly transformed into the first embryo-cell.

The deservedly great authority of the late Johannes Müller may be cited on the same side—so far, at least, as that singular mollusk, *Entoconcha mirabilis*, is concerned.

Dr. Gegenbaur affirms the occurrence of a similar process to be the rule among the *Calycophoridæ*, *Physophoridæ*, and certain other *Hydrozoa*, and in that singular annulose animal, *Sagitta*. Thus, in describing the development of *Oceania armata* (Zur Lehre vom Generationswechsel, 1854, p. 28), Gegenbaur says (the italics are his own):—

"Every act of division is preceded by a division of the nucleus, and consequently the first act by the *division of the germinal vesicle*: (the transparency of the yelk allows of the most precise observation of all these phenomena, and the following of *the development of the nuclei of the later embryo-cells out of the original germinal vesicle* (the nucleus of the primitive ovi-cell)."

Again, at p. 50 of his "Beiträge zur näheren Kenntniss der Schwimmpolypen" (1854), the same author remarks, in giving an account of the development of these *Calycophoridæ* and *Physophoridæ*:—

"A process which may be here traced with particular clearness is the constant *division of the germinal vesicle, which precedes the*

division of the yelk; and the products of the division of the germinal vesicle behave similarly, in relation to the subdivision of the yelk-masses. I observed this process of yelk-division in *Agalmopsis*, *Physophora*, *Forskalia*, *Hippopodius*, and *Diphyes*, without noticing any important differences among them."

Leydig expresses the same conclusion, though more guardedly, in his account of the development of the ova of *Notommata Sieboldii*[1] :—

"The nuclei of the division-masses are very clear; and it appeared to me *as if the homogeneous, clear nucleus of the ripe ovum (the germinal vesicle) stood in a genetic relation to the nuclei of the division-masses—i. e.*, gave rise to them by immediate division. The ovum is, in fact, more transparent than in other *Rotifera*; and I have observed the absence of the germinal vesicle."

In a subsequent passage Dr. Leydig adverts to these observations as having inclined him to alter his previously entertained opinions respecting the fate of the germinal vesicle.

So far as the *Vertebrata* are concerned, such evidence as we possess as to the independent origin of the embryo-cells appears to be altogether of the weakly negative sort. I do not think it can be said that there is adequate foundation for the general assumption that the contents of the germinal vesicle take no direct share in their production; on the contrary, as respects the Frog, I find definite evidence tending to a contrary conclusion. Prevost and Dumas, and Von Bär, as is well known, proved the existence of a canal leading from the centre of the dark part of the Frog's egg to a cavity which Von Bär considered to be the seat of the germinal vesicle. Newport (Phil. Trans. 1851) described and figured this canal and cavity, and showed that the germinal vesicle is, in the ovarian ovum, lodged in the cavity. The vesicle is said to be dense, white, and opaque, and its interior to be full of secondary cells[2]. Newport affirms that no trace of the vesicle is to be found in ova that have left the ovary, but that an accumulation of white nucleated cells sometimes occupies its place, in ova which are in the act of leaving the ovary.

Remak (Entwickelung der Wirbelthiere, 1855), apparently unacquainted with Newport's observations, doubts whether the cavity down to which the canal leads, and which he terms Von Bär's 'Kernhöhle,' contains the germinal vesicle, though he inclines to the opinion that it does. But it is a most important circumstance

[1] "Ueber den Bau und die systematische Stellung der Räderthiere." Siebold und Kölliker's Zeitschrift, 1855.

[2] Newport, it should be observed, used the term 'cell' not very critically. But ten years ago, cell-worship had attained its culminating point.

that he proves (*l. c.* p. 137) that the division of this cavity accompanies each division of the yelk-mass, and that, eventually, these cavities become what he terms the nuclei provided with nucleoli, which occupy the centres of the division-masses of the yelk, and are the homologues of the embryo-cells of *Ascaris*. If both Newport's and Remak's observations are correct, it would seem impossible to deny that the embryo-cells of the Frog proceed from the contents of the germinal vesicle.

I think, then, that considering the only case in which the contents of the germinal vesicle are not traceable, under circumstances in which it might be reasonably expected that, if they really exist, they should be visible, is that observed by Kölliker; while, on the other hand, the equally definite observations of Nelson, Müller, Gegenbaur, and myself (and the less distinct evidence of Newport, Remak, and of Leydig) testify to the origin of the blastoderm in one way or the other from the contents of the germinal vesicle, in various members of no less than four[1] out of the five primary divisions of the animal kingdom; the balance of the evidence is in favour of the conclusion that the embryo-cells are the progeny of another cell, and that here, as elsewhere, extracellular cell-development is a phenomenon of rare, if not of altogether questionable, occurrence.

8, 9, 10. Thus far the problem has been to find a parallel for those early embryogenetic processes which are ordinarily common to large assemblages of living beings. Analogies for the more special modifications which the blastoderm undergoes may be sought for in the group of which the genus *Pyrosoma* forms a part. In the first place, it may be asked, are there, in this group, any examples of the division of the blastoderm into segments, one of which is to serve a temporary purpose, while the others become ascidiozooids?

Leaving the development of the caudal appendage of ordinary Ascidians out of consideration, as hardly a case in point, it yet appears that even in these Ascidians, the body of the embryo is, during its locomotive stage, divided into two segments, the anterior of which gives rise to the so-called suckers (which are diverticula of its wall with involuted ends), while the posterior is the rudiment of the body.

Löwig and Kölliker, in their description of the compound larva of *Botryllus* (originally discovered and described by Sars), consider the three processes which are given off from the "large round

[1] *Cœlenterata, Mollusca, Annulosa, Vertebrata.* I may add, that the first appearance of the blastoderm on the surface of the ovisac of *Pyrosoma* is so like that of the blastoderm in the ovum of any of the higher *Articulata*, as strongly to suggest a similarity of origin.

'mamelon' provided with an orifice" as the homologues of the three processes given off from the anterior division of the larval body in the simple Ascidians. In this case this 'mamelon,' which they consider to be the rudiment of the cloaca, must correspond with that anterior division. But the examination of their figures and descriptions renders it hardly doubtful to my mind that the 'mamelon' is a structure homologous with the cyathozooid of the fœtal *Pyrosoma*, the eight rudimentary ascidiozooids of the *Botryllus* being arranged around its base, just as the four are disposed in the fœtal *Pyrosoma*. If this reasoning be correct, it follows that the cyathozooid of *Pyrosoma* corresponds with the anterior division of the body in the ordinary Ascidian larva, *e.g.* of *Clavelina.*

The peculiar connexion of the embryo *Pyrosoma* with its ovisac, and the extrusion of the latter combined with the embryo, as a single fœtus, into the mid-atrium of the parent, are, however, peculiarities for which we should in vain seek a parallel among ordinary Ascidians. But there is one family of this class, the *Salpæ*, which resemble *Pyrosoma* in having an elæoblast, and in possessing no caudal appendage in the larval state (differing in the same respects from all other Ascidians), in which the search for analogies is more hopeful.

Most *Salpæ*, like *Pyrosoma*, possess, as Krohn was the first to point out, but a single ovisac, connected by a peduncle-like duct with the wall of the mid-atrium. Prof. Leuckart, who, with a knowledge of all that had been written upon the question, subjected the reproductive processes of the *Salpæ* to a renewed and very careful scrutiny, some years ago[1] stated (*l. c.* p. 47) that the ovum of *Salpa mucronata* consists of a granular, tolerably viscid yelk, enclosing a large, vesicular germinal vesicle, with a simple germinal spot. No vitelline membrane was to be detected,—the only covering of the ovum being the ovisac, which is closely applied to the surface of the vitellus, and is lined internally with a layer of small nucleated cells. The peduncle of the ovisac is a short, narrow duct, which only becomes a little thicker at its anterior end and, like the ovisac, is lined by an epithelium. Its anterior end opens into the atrium; and in the vicinity of the aperture the inner tunic exhibits an elongated, discoid thickening, in which numerous small nucleated cells, like those in the ovisac and its duct, are to be detected. This description, it is obvious, would apply equally well to the young ovisac of *Pyrosoma.*

It does not appear that the entrance of the spermatozoa into the duct of the ovisac has been observed in the *Salpæ.*

I have stated in my Memoir already cited (Phil. Trans. 1851

[1] Zoologische Untersuchungen, Zweites Heft, Salpen u. Verwandte. Giessen, 1854.

p. 577), that in a more advanced stage, probably after fecundation, the ovisac (which I called ovum) appears like a cellular mass. H. Müller (Siebold and Kölliker's Zeitschrift, iv. p. 331) speaks of the occurrence of yelk-division at this stage, without, however, describing that process more particularly. Vogt did not observe it, nor does Leuckart add much to our information on this head :—

"I can say little more about it [yelk-division] than that it begins during the change of place of the ovum (as H. Müller has also observed), and, as in the allied Ascidians, is a total yelk-division. When it has arrived in the fœtal chamber (Brutsack), the yelk exhibits the well-known mulberry appearance" (*l. c.* p. 52).

It is unfortunate that these observations are not so precise and detailed as they might have been ; for the question at once suggests itself, is this appearance presented by the ovisac really due to yelk-division ? What has become of the epithelium of the ovisac ? Might not the change in the appearance of the latter be due to an alteration in the character of the epithelium, similar to that which obtains in *Pyrosoma ?*

The next steps in the development of *Salpa* are, as I pointed out in 1851 (*l. c.* pp. 575–577), the enlargement of the ovisac, the shortening of its duct, and the consequent approximation of the ovisac to the atrial wall, and, finally, the protrusion of this part of the atrial wall into the atrium, so as to form a chamber containing the ovisac. This the German observers term the "Brut-sack," which may be rendered "fœtal chamber."

Arrived in the fœtal chamber, I have said (*l. c.* p. 575) that the fœtus "becomes divided into two portions,—a larger turned towards the respiratory cavity, and which projects more and more into it, and a smaller, subspherical, turned towards and lying in the cavity of the sinus, and bathed by the parental blood." The former becomes the embryo, the latter the placenta.

Leuckart's description comes to the same result, but is much fuller in details (pp. 52, 53) :—

"When the vitelline mass has increased to about double its primitive diameter, and has become changed by continual division into numerous small division-masses about $\frac{1}{100}'''$ in diameter, it loses its spherical form. A circular constriction appears in it, by which its anterior end is marked off as a hump-like process. This constriction indicates the boundary between the fœtus and the placenta. The placenta is, at first, the more considerable of these two parts. It is, one may say, the remains of the vitelline mass (yelk-sac) which is left after the formation of the rudiment of the embryo, and now, instead

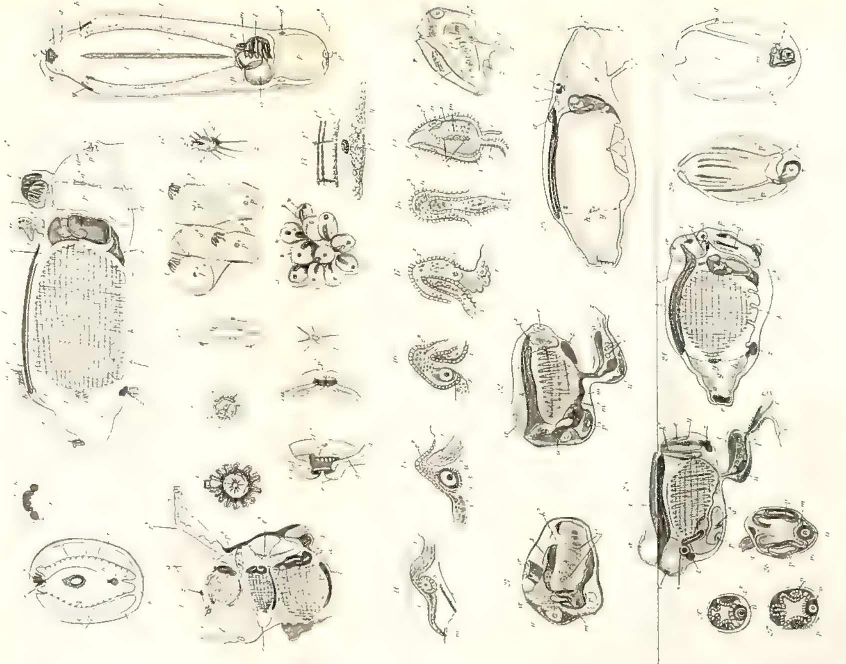
of being directly applied to developmental purposes, is metamorphosed into an accessory fœtal organ. . . . It has been mentioned above that the posterior segment of the yelk, in the fœtal chamber, is freely bathed by the blood of the parent. By the delimitation of the embryo, this segment has now become the posterior end of the placenta: at first, as a part of a spheroid, it naturally possessed a convex surface; but this disappears as soon as the first traces of embryonic development are visible. The posterior end of the placenta becomes flattened, and its centre acquires a depression, which penetrates deeper and deeper into its substance. The placenta loses its originally solid character, and (even before there is any marked change in the embryo) becomes rapidly metamorphosed into a cupola-like structure, whose internal cavity is connected by its posterior aperture with the circulatory apparatus of the parent, and may be regarded as a sinus for its blood. The inner walls, freely bathed by this blood, exhibit many irregular elevations, which for the most part run, like ribs, from the apex of the cupola to its entrance. Not uncommonly there is also a conical process, which projects from the roof of the cupola for a greater or less distance into the cavity."

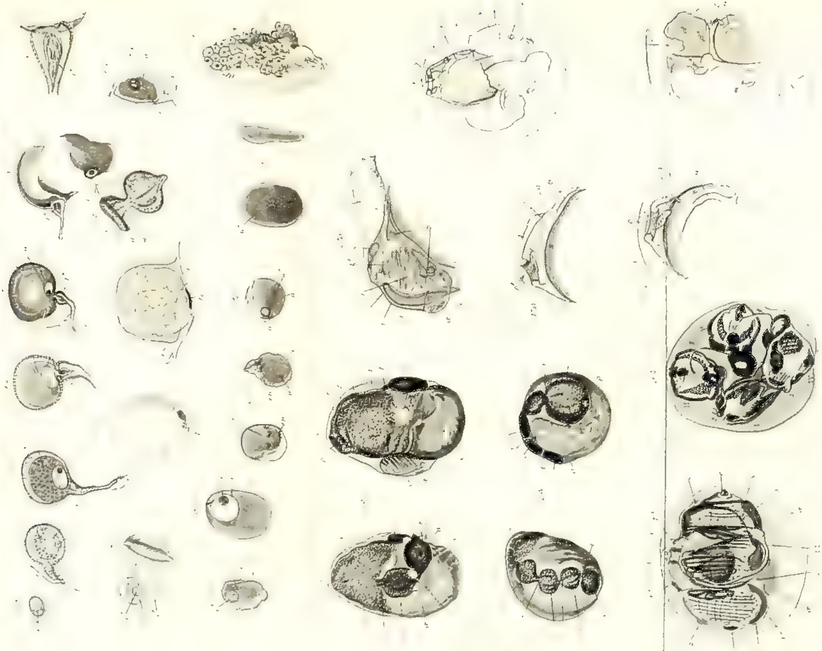
Vogt (Bilder aus dem Thierleben, p. 79 *et seq.*) gives an essentially similar account of the development of the placenta of *Salpa pinnata*[1]. Eventually the fœtus makes its way through the wall of the atrium, and, carrying its placenta with it, lies free in that cavity, whence it must shortly be expelled.

On the face of the matter, there appears to be a close analogy between this process and the development of the fœtus of *Pyrosoma*; for the projection of the atrial wall, caused by ovisacs in which the blastoderm is just appearing, may be fairly compared with the commencing fœtal chamber; while, if there were only one ascidiozooid instead of four, its relation to the cyathozooid would be very similar to that which the embryo of *Salpa* has to its placenta. Nor is there wanting a very considerable resemblance in form and character between the cyathozooid and the placenta.

But so much remains to be done before the developmental history of *Salpa* can be said to be fully made out, that I do not know how far these apparent resemblances may be depended upon as affording evidence of real similarity between the developmental histories of *Pyrosoma* and of *Salpa*. Vogt, Müller, and Leuckart seem, as little

[1] On the other hand, the description and figures by H. Müller, in the 'Icones Zootomicæ' of Prof. J. V. Carus, tab. 18, lead me to suspect the existence of differences in the development of the placenta in this species.





as myself, to have endeavoured to trace the fate of the ovisac and of its epithelium. And yet, with the development of *Pyrosoma* before me, it is impossible to arrive at a conclusion in the absence of information on this head. The long retention of the fœtus of *Salpa* in connexion with the parent and nourished by its blood, in contrast to the early separation of the fœtus of *Pyrosoma* and the turning of its cyathozooid to account in another way, leads me to conceive that considerable differences will be found in the details of their development, though I suspect further inquiry will prove that, in essentials, they are very similar.

EXPLANATION OF THE PLATES.

Plates XXX. [Plate 29] and XXXI. [Plate 30.]

The following letters and figures have the same signification throughout.

a, the test ; a^1, its oral ; a^2, its cloacal fibrillated layer ; a^3, labial processes of the ascidiozooids ; a^4, lip or so-called sphincter of the cloacal aperture ; a^5, cells of the embryonic test.
b, outer tunic.
c, inner tunic, or intestinal wall.
d, atrial tunic.
e, oral aperture.
f, tentacular membrane ; f^1, hæmal tentacle.
g, g^1 anterior muscles ; g^2, posterior or atrial muscles.
h, peripharyngeal ridge.
i, endostyle.
i, epipharyngeal folds.
k, hypopharyngeal band and sinus ; k^1, languets ; k^2, diapharyngeal band.
l, branchial sac ; l^1, horizontal branchial bars ; l^2, perpendicular branchial bars ; l^3, stigmata.
m, alimentary canal ; m^1, œsophageal aperture ; m^2, œsophagus ; m^3 stomach ; m^4, intestine.
n, tubular organ, probably hepatic.
o, anus.
p, mid-atrium ; p^1, lateral atria ; p^2, atrial aperture.
r, heart ; r^1, sinuses ; r^2, stolons of the adult ascidiarium ; r^3, vascular bands, connecting the branchial sac with the parietal sinus ; r^4, stolons of the embryonic ascidiarium, or tetrazooid.
s, ovisac ; s^1, its duct ; s^2, lining of the ovisac.
t, testis ; t^1, vas deferens ; t^2, spermatozoa.
u, yelk ; u^1 germinal vesicle ; u^2 germinal spot ; u^3, contents of the germinal vesicle.
w, bud ; w^1, its peduncle.
x, alimentary or trophic blastema of the nascent bud ; x^1, its generative blastema ; x^2, its tegumentary blastema.
y, the circular cellular patch, probably a renal organ.
z, the ganglion ; z^1, nerves ; z^2, the ciliated sac ; z^3, the tubercle.
æ, elæoblast.
en, embryonic endoplasts within the germinal vesicle.
bl. blastoderm.
cl, cloaca.

I. II. III. IV. V. Segments of the blastoderm. I. Cyathozooid. II.–V. Ascidiozooids.
1, 2, 3, 4, isthmuses.
β, the mouth of the cyathozooid, as formed by the test, and which becomes the future lip or 'sphincter' of the cloacal aperture; β^1, aperture of the cyathozooid when separated from the foregoing.
γ, cavity of the cyathozooid.
δ, appendix of the cyathozooid.
θ, canal connecting the first isthmus with the cavity of the cyathozooid.

PLATE XXX. [PLATE 29].

Fig. 1. A side view of a single ascidiozooid from the middle of the ascidiarium of *Pyrosoma giganteum*.
Fig. 2. A transverse and vertical section of the middle of the branchial region of a similar ascidiozooid exhibiting, in addition, the oral aperture, anterior muscles, peripharyngeal ridge, ganglia, and anterior end of the endostyle. There are more vascular bands (r^3) represented than would be seen in any one transverse section.
Fig. 3. A transverse and horizontal section of an ascidiozooid, without any labial process. It should be understood that s and t lie altogether above the intestine, and hence do not interrupt the communication between p and p^1 p^1.
Fig. 4. A vertical section of the wall of the ascidiarium, near the cloacal aperture and including its lip.
Fig. 5. View of part of the closed end of the ascidiarium, showing the four ascidiozooids (* * * *) which form its apex.
Figs. 6 & 6*a*. The oral aperture viewed from within and from the side.
Figs. 7 & 7*a*. The atrial aperture viewed under the same aspects.
Fig. 8. A transverse and vertical section of the middle of the hæmal region of the branchial sac, showing the endostyle and the parts adjacent.
Fig. 9. Part of the wall of the middle of the ascidiarium viewed from within, or from the cloacal side.
Fig. 10. The cloacal fibrillated layer.
Fig. 11. A cell of the general substance of the test.
Fig. 12. The nervous ganglion viewed from above.
Fig. 13. A section of the body-wall of an adult ascidiozooid, taken through the 'urinary' organ. l^4 indicates a minute depression which I was at one time inclined to regard as an aperture into the parietal sinus over this organ; but I suspect it is only a nascent stigma.
Fig. 14. The youngest condition of a bud, before the external tunic is elevated.
Figs. 15–20. Successive stages of development of the buds described in the text.
Fig. 21. A bud laid open by a vertical cut, and exhibiting an interior view of the branchial sac.
Fig. 22. A more advanced bud, with a second bud forming in its peduncle.
Fig. 23. A still more advanced terminal bud, a second median bud in about the same stage as fig 20, and a third proximal bud developing in the peduncle and nearly in the same stage as fig. 17, all connected together.
Fig. 24. A bud naturally detached from its peduncle, and exhibiting a rudiment of the stolon, r^2.
Fig. 25. A bud so far advanced as to be connected with the cloaca by its atrial aperture, p^2.
Figs. 26 & 27. Very young buds viewed from the side to which their apices are turned.
Figs. 28 & 29. More advanced buds viewed from the hæmal side.
Fig. 30. A still more advanced bud viewed from the hæmal side, and given partly in section, to compare with fig. 3.

PLATE XXXI. [PLATE 30].

Figs. 1, 2, 3, & 4. Ovisacs containing complete ova in different stages of development. The fraction above each figure gives the greatest diameter in parts of an inch.

Fig. 5. An ovisac, torn at one point, but otherwise entire, and allowing the naked germinal vesicle to be seen through its wall.

Fig. 6. A similar ovisac opened with needles, and the torn lower portion, to which the germinal vesicle adheres, viewed from within.

Fig. 6 *a*. An enlarged view of the germinal vesicle.

Fig. 6 *b*. A similarly magnified view of the dilated end of the duct of the same specimen, showing the 'plug' of spermatozoa.

Fig. 7. A more advanced ovisac opened and viewed from within, showing the pale germinal vesicle covered by the epithelial coating of the sac.

Fig. 8*. An ovum extracted from a younger ovisac than the last.

Figs. 8–8*c*. Germinal vesicles containing the characteristic deposit o. more advanced stages.

Fig. 8 *a* A germinal vesicle with a very pale spot. Its contour is rather too well defined in the figure.

Fig. 8 *b*. Two views of the same germinal vesicle, whose spot has disappeared. The minute vesicular corpuscles, *en*, are visible.

Fig. 8 *c*. Front and lateral views of a germinal vesicle in a condition observed once.

Fig. 9. Ovisac with vesicular epithelial lining and commencing blastoderm (which is represented rather darker than in nature) *in situ* and causing the atrial tunic, *d*, to bulge as a rudimentary 'Brutsack' or fœtal chamber.

Fig. 9. *a*. The blastoderm of a similar specimen enlarged, and viewed through the *tunica propria* of the ovisac. To avoid confusion, the texture of the vesicular lining is omitted.

N.B. The figures 8, 8*, 8 *a*, 8 *b*, 8 *c*, 9 *a*, are drawn to the same scale.

Fig. 10. Fœtus, now free in the mid-atrium, with the blastoderm much enlarged and converted into an elongated patch.

Fig. 11. Two views of a fœtus with the blastoderm divided into five segments, of which the cyathozooid is the largest.

Fig. 12. The fourth ascidiozooid of a similar ıœtus, seen in section, and the fifth from above.

Fig. 13. Two views of a fœtus whose ascidiozooids half encircle the base of its cyathozooid.

Fig. 13 *a*. A single ascidiozooid (the first) of a similar fœtus, seen from the side.

Fig. 14. A more advanced fœtus, to show the stage in which the ascidiozooids (left in outline) completely encircle the cyathozooid, but still lie below the level of the equator of the ovisac.

Fig. 15. One of the most advanced fœtuses observed. The remains of the conjoined cyathozooid and ovisac are hidden by the ascidiozooids.

Fig. 16. A similar fœtus viewed from above, to show the remains of the cyathozooid and the ovisac, as well as the connexion of this with the ascidiozooids, and of these with one another by the elongated isthmuses.

Figs. 17 & 18. Lateral views of the cyathozooid in fœtuses $\frac{1}{21}$th and $\frac{1}{13}$th of an inch in diameter respectively.

Fig. 19. Lateral view of a fœtus $\frac{1}{21}$st of an inch in diameter, to show the manner in which the cloaca is developed by the separation of the test from the combined cyathozooid and ovisac.

XVIII

ON SPECIES AND RACES, AND THEIR ORIGIN

Proceedings of the Royal Institution of Great Britain, vol. iii. 1858–62, *pp.* 195–200. (*Friday, February* 10, 1860.)

THE speaker opened his discourse by stating that its object was to place the fundamental propositions of Mr. Darwin's work "On the Origin of Species by Natural Selection," in a clear light, and to consider whether, as the question at present stands, the evidence adduced in their favour is, or is not, conclusive.

After some preliminary remarks, in the course of which the speaker expressed his obligations for the liberality with which Mr. Darwin had allowed him to have access to a large portion of the MSS. of his forthcoming work, the phenomena of species in general were considered—the Horse being taken as a familiar example. The distinctions between this and other closely allied species, such as the Asses and Zebras, were considered, and they were shown to be of two kinds, structural or morphological, and functional or physiological Under the former head were ranged the callosities on the inner side of the fore and hind limbs of the Horse—its bushy tail, its peculiar larynx, its short ears, and broad hoofs; under the latter head, the fact that the offspring of the horse with any of the allied species is a hybrid, incapable of propagation with another mule, was particularly mentioned.

Leaving open the question whether the physiological distinction just mentioned is, or is not, a universal character of species, it is indubitable that it obtains between many species, and therefore has to be accounted for by any theory of their origin.

The species *Equus caballus*, thus separated from all others, is the centre round which a number of other remarkable phenomena are

grouped. It is intimately allied in structure with three other members of the existing creation, the Hyrax, the Tapir, and the Rhinoceros; and less strait, though still definite bonds of union connect it with every living thing. Going back in time, the Horse can be traced into the Pliocene formation, and perhaps it existed earlier still; but in the newer Miocene of Germany it is replaced by the *Hippotherium*, an animal very like a true *Equus*, but having the two rudimental toes in each foot developed, though small. Further back in time, in the Eocene rocks, neither *Equus* nor *Hippotherium* have been met with, nor *Rhinoceros*, *Tapirus*, or *Hyrax*; but instead of them, a singular animal, the *Palæotherium*, which exhibits certain points of resemblance with each of the four existing genera, is found. The speaker pointed out that these resemblances did not justify us in considering the *Palæotherium* as a more generalized type, any more than the resemblance of a father to his four sons justifies us in considering him as of a more generalized type than theirs.

The geographical distribution of the *Equidæ* was next considered; and the anomalies and difficulties it offers were pointed out; and lastly the variations which horses offer in their feral and their domesticated condition, were discussed.

The questions thus shown to be connected with the species Horse, are offered by all species whatever; and the next point of the discourse was the consideration of the general character of the problem of the origin of species of which they form a part, and the necessary conditions of its solution.

So far as the logic of the matter goes, it was proved that this problem is of exactly the same character as multitudes of other physical problems, such as the origin of glaciers, or the origin of strata of marble; and a complete solution of it involves—1. The experimental determination of the conditions under which bodies having the characters of species are producible; 2. The proof that such conditions are actually operative in nature.

Any doctrine of the origin of species which satisfies these requirements must be regarded as a true theory of species; while any which does not, is, so far, defective, and must be regarded only as a hypothesis whose value is greater or less, according to its approximation to this standard.

It is Mr. Darwin's peculiar merit to have apprehended these logical necessities, and to have endeavoured to comply with them. The Pigeons called Pouters, Tumblers, Fantails, &c., which the audience had an opportunity of examining, are, in his view, the result of so many long-continued experiments on the manufacture of species; and

he considers that causes essentially similar to those which have given rise to these birds are operative in nature now, and have in past times been the agents in producing all the species we know. If neither of these positions can be upset, Mr. Darwin's must be regarded as a true theory of species, as well based as any other physical theory: they require, therefore, the most careful and searching criticism.

After pointing out the remarkable differences in structure and habits between the Carrier, Pouter, Fantail, Tumbler, and the wild *Columba livia*, the speaker expressed his entire agreement with Mr. Darwin's conclusion, that all the former domesticated breeds had arisen from the last-named wild stock; and on the following grounds— 1. That all interbreed freely with one another. 2. That none of the domesticated breeds presents the slightest approximation to any wild species but *C. livia*, whose characteristic markings are at times exhibited by all. 3. That the known habits of the Indian variety of the Rock Pigeon (*C. intermedia*) render its domestication easily intelligible 4. That existing varieties connect the extremest modifications of the domestic breeds by insensible links with *C. livia*. 5. That there is historical evidence of the divergence of existing breeds, *e.g.*, the Tumbler, from forms less unlike *C. livia*.

The speaker then analyzed the process of selection by which the domesticated breeds had been produced from the Wild Rock Pigeon; and he showed its possibility to depend upon two laws which hold good for all species, viz., 1. That every species tends to vary. 2. That variations are capable of hereditary transmission. The second law is well understood; but the speaker adverted to the miscomprehension which appears to prevail regarding the first, and showed that the variation of a species is by no means an adaptation to conditions in the sense in which that phrase is commonly used. Pigeon-fanciers in fact, subject their pigeons to a complete uniformity of conditions; but while the similarly used feet, legs, skull, sacral vertebræ, tail feathers, oil gland and crop undergo the most extraordinary modifications; on the other hand, the wings, whose use is hardly ever permitted to the choice breeds, have hitherto shown no sign of diminution. Man has not as yet been able to determine a variation; he only favours those which arise spontaneously, *i.e.*, are determined by unknown conditions.

It must be admitted that, by selection, a species may be made to give rise experimentally to excessively different modifications; and the next question is: Do causes adequate to exert selection exist in nature? On this point, the speaker referred his audience to

Mr. Darwin's chapter on the struggle for existence, as affording ample satisfactory proof that such adequate natural causes do exist.

There can be no question that just as man cherishes the varieties he wishes to preserve, and destroys those he does not care about; so nature (even if we consider the physical world as a mere mechanism) must tend to cherish those varieties which are better fitted to work harmoniously with the conditions she offers, and to destroy the rest.

There seems to be no doubt then, that modifications equivalent in extent to the four breeds of pigeons, might be developed from a species by natural causes; and, therefore, if it can be shown that these breeds have all the characters which are ever found in species, Mr. Darwin's case would be complete. However, there is as yet no *proof* that, by selection, modifications having the physiological character of species (*i.e.*, whose offspring are incapable of propagation, *inter se*) have ever been produced from a common stock.

No doubt the numerous indirect arguments brought forward by Mr. Darwin to weaken the force of this objection are of great weight; no doubt it cannot be proved that all species give rise to hybrids infertile, *inter se*; no doubt (so far as the speaker's private conviction went), a well conducted series of experiments very probably would yield us derivatives from a common stock, whose offspring should be infertile, *inter se*: but we must deal with facts as they stand; and at present it must be admitted that Mr. Darwin's theory does not account for all the phenomena exhibited by species; and so far, falls short of being a satisfactory theory.

Nevertheless the speaker expressed his sense of the extremely high value to be attached to Mr. Darwin's hypothesis; and, avowing his own conviction that the following it out must ultimately lead us to the detection of the laws which have governed the origin of species, he concluded his discourse in the following words, which he wishes to be added in full to the very brief preceding account of his view of Mr. Darwin's argument:—

"I have endeavoured to lay before you what, as I fancy, are the turning points of a great controversy; to render obvious the mode in which the vast problem of the origin of species must be dealt with; and so far as purely scientific considerations go, I have nothing more to say. But let me beg you still to listen to a last word respecting the unscientific objections which I constantly hear brought forward on the part of the general public, against such doctrines as those we have been discussing. For this is a matter upon which it is of the utmost importance that men of science and the public should come to an understanding. I have heard it said that it is presumptuous for

us to attempt to inquire into such matters as these; that they are problems beyond the reach of the human understanding. Do you remember what was the reply of the old philosopher to those who demonstrated to him so clearly the impossibility of motion? 'Solvitur ambulando,' said he, and got up and walked. And so I doubt not that one of these days either Mr. Darwin's hypothesis, or some other, will get up and walk, and that vigorously; and so save us the trouble of any further discussion of this objection.

"Another, and unfortunately a large class of persons take fright at the logical consequences of such a doctrine as that put forth by Mr. Darwin. If all species have arisen in this way, say they—Man himself must have done so; and he and all the animated world must have had a common origin. Most assuredly. No question of it.

"But I would ask, does this logical necessity add one single difficulty of importance to those which already confront us on all sides whenever we contemplate our relations to the surrounding universe? I think not. Let man's mistaken vanity, his foolish contempt for the material world, impel him to struggle as he will, he strives in vain to break through the ties which hold him to matter and the lower forms of life.

"In the face of the demonstrable facts, that the anatomical difference between man and the highest of the *Quadrumana* is less than the difference between the extreme types of the Quadrumanous order; that, in the course of his development, man passes through stages which correspond to, though they are not identical with, those of all the lower animals: that each of us was once a minute and unintelligent particle of yolk-like substance; that our highest faculties are dependent for their exercise upon the presence of a few cubic inches, more or less, of a certain gas in one's blood; in the face of these tremendous and mysterious facts, I say, what matters it whether a new link is or is not added to the mighty chain which indissolubly binds us to the rest of the universe? Of what part of the glorious fabric of the world has man a right to be ashamed—that he is so desirous to disconnect himself from it? But I would rather reply to this strange objection by suggesting another line of thought. I would rather point out that perhaps the very noblest use of science as a discipline is, that now and then she brings us face to face with difficulties like these. Laden with our idols, we follow her blithely—till a parting in the roads appears, and she turns, and with a stern face asks us whether we are men enough to cast them aside, and follow her up the steep? Men of science are such by virtue of having answered her with a hearty and unreserved, Yea; by virtue of having

made their election to follow science whithersoever she leads, and whatsoever lions be in the path. Their duty is clear enough.

"And, in my apprehension, that of the public is not doubtful. I have said that the man of science is the sworn interpreter of nature in the high court of reason. But of what avail is his honest speech if ignorance is the assessor of the judge, and prejudice foreman of the jury? I hardly know of a great physical truth, whose universal reception has not been preceded by an epoch in which most estimable persons have maintained that the phenomena investigated were directly dependent on the Divine Will, and that the attempt to investigate them was not only futile, but blasphemous. And there is a wonderful tenacity of life about this sort of opposition to physical science. Crushed and maimed in every battle, it yet seems never to be slain; and after a hundred defeats it is at this day as rampant, though happily not so mischievous, as in the time of Galileo.

"But to those whose life is spent, to use Newton's noble words, in picking up here a pebble and there a pebble on the shores of the great ocean of truth—who watch, day by day, the slow but sure advance of that mighty tide, bearing on its bosom the thousand treasures wherewith man ennobles and beautifies his life—it would be laughable, if it were not so sad, to see the little Canutes of the hour enthroned in solemn state, bidding that great wave to stay, and threatening to check its beneficent progress. The wave rises and they fly; but unlike the brave old Dane, they learn no lesson of humility: the throne is pitched at what seems a safe distance, and the folly is repeated.

"Surely it is the duty of the public to discourage everything of this kind, to discredit these foolish meddlers who think they do the Almighty a service by preventing a thorough study of his works.

"The Origin of Species is not the first, and it will not be the salt of the great questions born of science, which will demand settlement from this generation. The general mind is seething strangely, and to those who watch the signs of the times, it seems plain that this nineteenth century will see revolutions of thought and practice as great as those which the sixteenth witnessed. Through what trials and sore contests the civilized world will have to pass in the course of this new reformation, who can tell?

"But I verily believe that come what will, the part which England may play in the battle is a grand and a noble one. She may prove to the world that for one people, at any rate, despotism and demagoguy are not the necessary alternatives of government; that freedom and order are not incompatible; that reverence is the handmaid of know-

ledge; that free discussion is the life of truth, and of true unity in a nation.

"Will England play this part? That depends upon how you, the public, deal with science. Cherish her, venerate her, follow her methods faithfully and implicitly in their application to all branches of human thought; and the future of this people will be greater than the past.

"Listen to those who would silence and crush her, and I fear our children will see the glory of England vanishing like Arthur in the mist; they will cry too late the woful cry of Guinever:

> 'It was my duty to have loved the highest
> It surely was my profit, had I known;
> It would have been my pleasure had I seen.'

XIX

ON THE STRUCTURE OF THE MOUTH AND PHARYNX OF THE SCORPION

Quarterly Journal of Microscopical Science, vol. viii., 1860, *pp.* 250—254.

ALTHOUGH the scorpion has been made the subject of repeated investigations by some of the best minute anatomists of past and present times, it is a remarkable circumstance that no exact account of the structure of the commencement of its alimentary canal is to be met with, at least so far as my knowledge extends. Meckel ('Beiträge zur Vergleichenden Anatomie,' Band i, Heft 2, 1809), as might be expected from the fact that his dissections were performed without the aid of even a magnifier (page 106), takes no particular notice of the small and delicate parts in question. Treviranus ('Bau der Arachniden,' 1812) is equally silent as to this important portion of the economy of the scorpion; and even the accurate Johannes Müller, in the essay entitled "Beiträge zur Anatomie des Scorpions" (Meckel's 'Archiv.,' 1828), which threw so much new light upon the organization of this animal, although he saw more than either his predecessors or his successors have done, did not probe the matter to the bottom. In describing the alimentary canal, he merely says:—"The pharynx which arises in front of the brain, upon a particular, strongly excavated, portion of the skeleton, is much wider than the rest of the intestine, and resembles a vesicle. The œsophagus is very delicate where it proceeds from this vesicle, rises between the very stout nerves for the chelæ, above the brain (which lies behind the pharynx), and passes over the saddle-shaped upper excavation of the internal thoracic skeleton, whilst the spinal cord and the posterior cerebral nerves pass through the opening of the same skeleton."

Even the elaborate and beautifully illustrated memoir on the organization of *Scorpio occitanus*, published by M. Blanchard, a couple of years ago,[1] does not furnish the inquirer with either definite or accurate information on this point. At page 19, I find under the head of "*mouth*":

"In the scorpion there exists only a single buccal piece properly so called; it is inserted in the median line above (*au-dessus*) the mouth, just below the cheliceræ (*antennes pinces*), and wedged in, so to speak, between the foot-jaws. It is a little flexible appendage, thinner towards its extremity, sensibly dilated laterally, convex above, and beset, chiefly at the end, with fine and silky hairs. This piece presents two apodemata (*apodèmes d'insertion*), which diverge greatly from one another.

"One finds a certain difficulty in positively determining the nature of the single buccal appendage of the scorpion. It is impossible to regard it as the analogue of the labrum (*lèvre supérieure*) of insects. The labrum is one of those pieces which abort most completely in the arachnida. Besides, in all articulata, this labrum receives nerves which arise from the cerebral ganglia. It is different with the buccal appendage of the scorpion; its nerves arise from the anterior part of the subœsophageal ganglia, exactly like those of the mandibles and maxillæ of Crustacea and Insects. It can thus only be compared to these pieces; but ought we to regard it as representing both the mandibles and the jaws, or only the mandibles, or the jaws, either one or the other being supposed to be aborted?"

With respect to both the main points contained in these paragraphs, however, M. Blanchard subsequently makes statements which seem difficult to harmonise with the conclusions enunciated.

Thus, at page 41, I find:

"The pharyngeal nerves are two pair. Those of the first take their origin from the anterior and median edge of the cerebrum, and almost immediately unite so as to form a single nerve, whose branches are distributed in the upper portion of the buccal appendage. It is evidently the analogue of the nerves of the labrum of insects."

And, again, at page 60:

"*Mouth and æsophagus.*—The buccal orifice appears under the form of a little transverse cleft, hidden under the cheliceræ *above* (*au-dessus*) the median appendage, which has already been described (p. 19); its edges are flexible, and are deprived of asperities. The œsophagus, which commences in a slightly funnel-shaped pharynx, is

[1] The livraisons of M. Blanchard's work are unfortunately published without dates.

delicate, short, and widened posteriorly, so as to resemble what M. Léon Dufour calls the 'jabot' in insects. The œsophagus is held upon each side, towards its middle, by a fine muscular band directed backwards, and towards its point of union with the stomach by a similar band directed forwards. These muscles are attached to the sternal floor, formed, as is known, by the basilar pieces of the appendages. They serve to stretch the œsophagus either forwards or backwards, so as to facilitate deglutition.

"The walls of the œsophagus are thin and smooth internally, and present a few fine folds."

In the figures (*op. cit.*, pl. iv, figs. 1 and 6), which represent the anterior part of the alimentary canal, the œsophagus is represented as a straight, taper tube, ending in the mouth, without change of direction.

At page 32, M. Blanchard states, under the head of—

"*Muscles of the buccal appendage.*—We have indicated the two, long, diverging, apodemes of this piece (p. 19). Upon the base of each of them is inserted an elevator muscle, provided with two fixed attachments to the cephalo-thoracic shield in front of and external to the median eyes (pl. ii, fig. 4 *e e* and fig. 6 *a*). By its contraction, this muscle causes the buccal appendage to be elevated a little—a movement which takes place when the animal introduces food into its mouth. A transverse muscle is attached to the two apodemic plates (pl. ii. fig. 4 *f*); it is this muscle which, acting either on the one side or on the other, determines the slight lateral movements of the buccal appendage. It is to be observed, that this piece, solidly fixed between the foot-jaws, sensibly involves the latter during the execution of its slight movements."

The structure of the parts which I have observed in a large species of *Buthus* may be described as follows:

The "buccal appendage" of M. Blanchard is a vertically elongated, laterally compressed, cushion-like prominence, broad and rounded above, where it is marked by a slight median ridge, slightly concave from above downwards in front, and narrowed below (Pl. XII, figs. 1, 2, 3 *b*). Its anterior and lateral surfaces are covered with fine, short hairs, which form a projecting pencil at its anterior inferior angle. There is no aperture whatsoever above this body, between the cheliceræ; but, below and behind it, the aperture of the mouth, large enough to admit the head of a fine needle, can be very easily found. I entertain no doubt, therefore, that this "buccal appendage" is a true labrum, and, indeed, in all essential respects, it is exactly like that part in the *crustacea*.

The convex lower surface of the labrum bounds the mouth in front, while behind, it is limited by a transverse thickening of the chitinous integument, which appears to represent the sternum of the mandibular somite (fig. 4 *o*). The mouth opens into a very curious pharynx, formed by a delicate outer investment, and a strong inner chitinous lining. Viewed laterally, this organ (*c*) has the shape of a pear, its broad end being uppermost, and its long axis directed obliquely upwards, and backwards, in such a manner, that the broad upper end lies in the middle, between the prongs of the fork-like apodeme, which M. Blanchard has described. Viewed from above or below, however, the pharynx appears to be very narrow, indeed, almost linear, in consequence of its very peculiar form, which is displayed in the section, taken transversely to the longitudinal axis and perpendicularly to the vertical plane represented in fig. 5. The cavity of the sac is here seen to be triradiate, while its walls are very closely approximated, so as to leave but a slight interspace. The narrow band which joins the two lateral walls below and behind is slightly excavated, so as to present a convexity towards the cavity of the pharynx. The two shorter rays of the sac are turned upwards and outwards; the third longer ray is directed vertically downwards. The œsophagus, an exceedingly delicate and narrow tube, comes off from the posterior wall of the vertical ray or crus of the pharynx, just above the mouth; and, widening, passes backwards and upwards, into the dilatation which receives the ducts of the so-called salivary glands (*e*). Just above the aperture is a rounded projection (fig. 6 *p*), which I suspect may act as a sort of valve, when the sides of the pharynx are divaricated, by more or less completely occluding the œsophageal aperture. The inner surface of the chitinous lining of the pharynx is more or less rugose: and, towards the œsophageal aperture, presents a number of very minute spines (fig. 6).

The transverse muscular fibres (fig. 2 *n*), rightly said by M. Blanchard to arise from the forks of the apodeme (*m*), are inserted into the side walls of the pharyngeal sac, which is so narrow from side to side, as readily to escape notice, without dissection. The termination of the aorta appeared to me to pass between the two superior crura of the sac.

The large vertical muscles (fig. 1 *q*) are, as M. Blanchard states, inserted into the base of the apodeme; and, besides these, the labrum is traversed by strong transverse and longitudinal muscles.

The mode of action of this curious apparatus appears to be readily intelligible. Scorpions, as is well known, suck the juices of their prey, and the pharyngeal sac seems to be well calculated to

[PLATE 31.]

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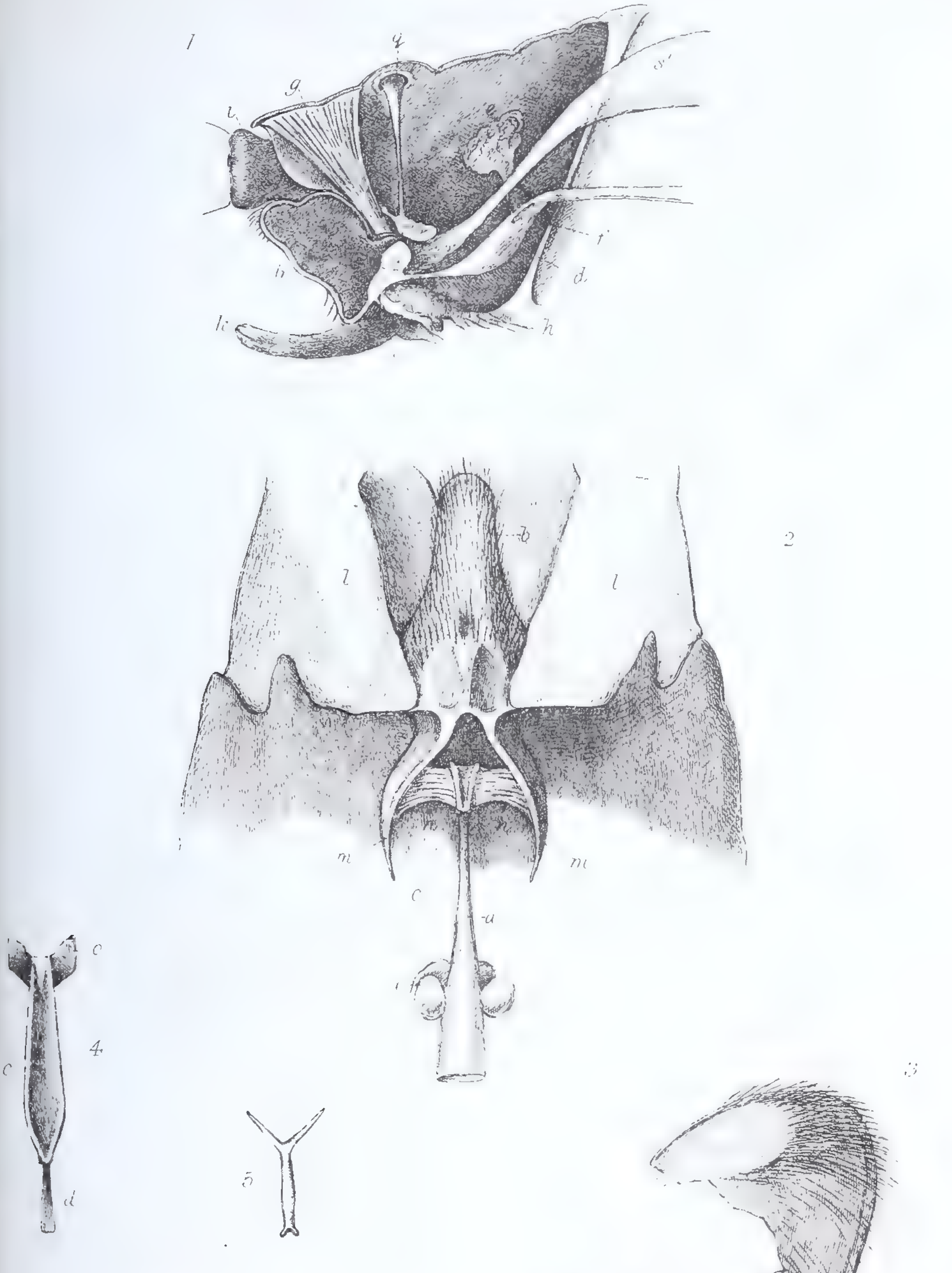

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perform the part of a kind of syringe. For, suppose the prey to be held between the labrum above, the bases of the great mandibles of the sides, and the processes furnished by the maxilliary limbs below, and that the minute oral aperture is applied to a wound. Then, if the transverse muscles (*n*) contract, the sides of the pharynx will be drawn apart, and a partial vacuum, or at least a tendency to the formation of one, will be created. If, by the same action, the projection (*p*) is brought down over the œsophageal aperture, regurgitation from the œsophagus will be prevented; but, in any case, as the oral aperture is larger than the œsophageal, it will be easier for the sac to be filled through the mouth. The sac being full, if the labrum is depressed so as to close the oral aperture, and the transverse muscles are relaxed, the elasticity of the walls of the pharynx will tend to reduce its cavity to its primitive dimensions, and hence to drive the ingested liquid into the œsophagus. Successive repetitions of the action would gradually pump the juices of the prey into the alimentary canal of its captor.

PLATE XII. [PLATE 31].

FIG.

1.—Longitudinal vertical section of the cephalo-thorax of a Scorpion, showing the pharynx, œsophagus, nervous centres, and the large eyes in their natural relations.

2.—Dorsal view of the cephalo-thorax of a Scorpion, opened and dissected, so as to show the apodemata, and the anterior portion of the alimentary canal, with the pharyngeal muscles.

3.—The chitinous lining of the anterior part of the alimentary canal, the integument of the labrum, and the basal processes of the first maxilla.

4.—The chitinous lining of the pharyngeal sac, viewed from above.

5.—A transverse section of the same, taken along the line *x y* (fig. 3).

6.—The region of the pharyngeal sac near the commencement of the œsophagus.

The letters have the same significations throughout:—*a*, mouth; *b*, labrum; *c*, pharynx; *d*, œsophagus; *e*, salivary duct; *f*, diaphragm; *g*, eye and ocular nerve; *h*, subœsophageal ganglion; *i*, antenna; *k*, maxilla; *l*, mandible; *m*, apodeme; *n*, pharyngeal muscles; *o*, sub-oral transverse thickening of the chitinous integument; *p*, valve (?) of the pharynx; *x y*, line along which the section in fig. 5 is taken.

XX

ON THE NATURE OF THE EARLIEST STAGES OF THE DEVELOPMENT OF ANIMALS

Proceedings of the Royal Institution of Great Britain, vol. iii. 1858–62, *pp.* 315–317. (*Fridav, February* 8, 1861.)

THE lecturer commenced by giving a general description of the structure and singular properties of the animal organism, termed *Pyrosoma Giganteum*, a specimen of which, taken by Capt. Callow in the North Atlantic, had been forwarded to him by Admiral Fitzroy, in the autumn of 1859.

Not only had his investigations enabled the speaker to verify the most important of the statements made in his memoir on *Pyrosoma*, published in the *Philosophical Transactions* for 1851; but they had revealed peculiarities in the mode of reproduction of the animal, of great interest from their bearing on some of the most difficult questions of embryology.

In order to render the importance of these new facts obvious, it was necessary to premise a concise statement of our present knowledge with regard to the early stages of animal development. To this end the structure of the fowl's egg was described, and the effects of incubation were traced, so far as was necessary to prove that the chick takes its origin from the cicatricula, or blastoderm.

It was next pointed out, that we owe the discovery of this important fact to the great Harvey, who, in his "Exercitationes de Generatione Animalium," demonstrated with perfect clearness, firstly, that the chick is developed from the cicatricula, and not, as had been supposed, from the chalazæ, or other parts; and secondly, that the process of development is an "epigenesis," or gradual addition of new parts to those already formed.

In virtue of these discoveries, Harvey has as much right to be regarded as the originator of modern embryology, as, in virtue of his discovery of the circulation, he has to be considered the founder of scientific physiology: but his embryological views met with a less fortunate reception than his physiological doctrines; and for a century and a half, the strange dogmas of the evolutionists, supported by the vast authority of Haller and of Cuvier, were allowed almost completely to override and weigh down the sounder teachings of the great Englishman.

With the publication of Caspar F. Wolff's "Theoria Generationis," in the middle of the last century, however, a new epoch commenced; and partly by the labours of that eminent observer, and still more largely by those of Pander, Von Bär, Rathke, and Reichert, Harvey's doctrine has been rehabilitated, and has taken its place among the firmly ascertained verities of science.

For want of proper microscopes and other appliances, neither Harvey nor C. F. Wolff could trace the origin of the germ further back than the blastoderm; still less could they obtain any just conception of the essential structure of the ovum. But in the course of the last thirty-five years, thanks to the labours of Purkinje, Von Bär, Wagner, Bischoff, Wharton Jones, Prevost, Dumas, Coste, and others, vast advances have been made.

It has been ascertained that the ovum of every animal primarily consists of a germinal vesicle, containing its so-called spot, and enclosed within a yelk, or vitellus; and that, in the great majority of cases, the first changes which follow upon impregnation consist in the disappearance of the germinal vesicle as such, and the regular division of the yelk into smaller and smaller masses, out of which, in one way or another, the blastoderm, of which the embryo is a modification, arises. Such yelk division, however, has not yet been observed among the higher *Annulosa*, nor in certain *Entozoa*, nor does it occur in *Pyrosoma*.

So much being definitely ascertained, there is yet one question upon which embryologists are widely divided, viz., What is the relation between the germinal vesicle and the cells, or structural elements, of which the blastoderm is composed? Three answers have been given to this question:—

1. According to the late Dr. Barry, the blastoderm arises from a modification of the germinal vesicle, in a manner particularly described by him. No other observer, however, has been able to discover a trace of this process; and it may be regarded as tolerably certain that its describer was mistaken.

2. According to Bischoff, Kölliker, and the majority of embryologists, the germinal vesicle and its contents disappear, and have no direct connection with the cells of the blastoderm.

3. According to observations of the late Johannes Müller, of Gegenbaur and others, the germinal vesicle may give rise directly, by division, to the cells of the blastoderm.

The study of the development of the embryo of *Pyrosoma* yields results in close conformity with the last view. The ovum of this animal is, in fact, composed, at first, like all others, of germinal vesicle, germinal spot, and vitellus; but, in the course of development, the vitellus disappears, probably becoming liquefied, and the germinal vesicle is laid bare, so that it becomes comparatively easy to watch the subsequent changes in its interior. These consist in the deposit of a somewhat opaque matter and the division of the germinal spot, so as to give rise to the endoplasts, or "nuclei" of the blastoderm, which is thus primarily formed within the interior of the germinal vesicle.

The speaker concluded by observing, that it is not improbable that the process thus traced, is similar to that by which the blastoderm of the higher *Annulosa* arises, and that it will probably furnish the key to the signification of the multiple germinal spots observed in so many of the lower *Vertebrata*; while, by proving the direct descent of some of the histological elements of the progeny from those of the parent, it combines the theories of the pre-existence of germs with that of epigenesis.

XXI

ON A NEW SPECIES OF MACRAUCHENIA (M. BOLIVIENSIS)

Quarterly Journal of the Geological Society of London, vol. xvii., 1861, *pp.* 73—84. (*Read November* 21, 1860.)

THE vertebrate remains obtained by David Forbes, Esq., F.R.S., F.G.S., from the mines at Corocoro, under the circumstances detailed in his paper "On the Geology of Bolivia and Southern Peru," consist of the following parts of the skeleton of apparently one and the same Mammal:—1. A portion of the right maxilla and palate, with fragments of grinding teeth. 2. Rather more than the right half of the occipital portion of the skull. 3. A middle cervical vertebra, nearly entire. 4. A fragment of a posterior lumbar vertebra. 5. A small portion of a right scapula. 6. A crushed fragment of the proximal end of an ulna. 7. Part of the proximal end of the left tibia. 8. The entire left astragalus, and part of the right astragalus. The bones are all in the same, and that a very peculiar, mineral condition—the Haversian canals being for the most part filled up with threads of native copper; so that the fossils are not only exceedingly dense, but, in consequence of their internal flexible metallic support, their thinner and more delicate parts bend, rather than break, when force is applied to them.

The characters of the cervical vertebra and of the astragalus, which are fortunately the best-preserved of all the fossils, at once demonstrated the remains to belong to the genus *Macrauchenia* (Owen), while the entire absence of epiphysial sutures in the vertebræ and the long bones, and of similar indications of immaturity in the fragment of the skull, proved the animal to have attained its adult condition. The vertebra and the astragalus, however, have not more than half the size of the corresponding bones of the species,

M. Patachonica, discovered by Mr. Darwin, and described by Professor Owen in the 'Appendix to the Voyage of the Beagle'; and as, in addition, these and the other bones present different proportions from those of the Patagonian species, I have no hesitation in regarding the fossils collected by Mr. Forbes as the remains of a distinct species, for which I propose the name of *Macrauchenia Boliviensis*. It will be convenient to commence the description of these fossils with those parts upon which the diagnosis of the species may be most safely rested, viz. the cervical vertebra and the astragalus.

The cervical vertebra (Plate VI. [Plate 32.] fig. 1).—The great length of the centrum of this vertebra, the peculiar form of its transverse processes, and the absence of perforations for the vertebral arteries in them are characters which, in the present state of knowledge, oblige the anatomist at once to refer it either to one of the existing *Camelidæ* or to the genus *Macrauchenia*; while the two strong, converging ridges which mark the posterior half of the under surface of the vertebra, and meet to form a single ridge, which dies away anteriorly in the middle of that surface, together with the slight concavity of both the posterior and the anterior articular faces of the centrum, are decisive in favour of the latter alternative. In fact, the excellent description of the cervical vertebræ of *Macrauchenia Patachonica* which has been given by Professor Owen applies so well to that of *M. Boliviensis*, that referring to the paper in the 'Appendix to the Voyage of the Beagle,' already cited, for a general account of the characters of Macrauchenian vertebræ, I shall content myself with pointing out the resemblances and differences of the Bolivian from the Patagonian *Macrauchenia*, and from the existing *Aucheniæ*. The dimensions of the centrum of the cervical vertebræ of the two *Macraucheniæ*, and of the fourth cervical of a Guanaco and of a Vicugna in the College of Surgeons' Museum are as follows:—

	M. Boliviensis.	*M. Patachonica.*	*Guanaco.*	*Vicugna.*
	in.	in.	in.	in.
Length	3·8	6·6	4·6	4·0
Width of anterior face .	1·1	3·2	1·1	·8
Width of posterior face	1·25	3·4	1·3	1·0

Thus it appears that the centrum of the cervical vertebra of *Macrauchenia Boliviensis* is far more slender than that of *M. Patachonica*; for, while the length of the former is to that of the latter as 1 : 1$\frac{7}{9}$, the transverse diameters of the anterior faces of the centra of the two species are, nearly, as 1 : 3. The cervical vertebra of the new species is, absolutely, rather shorter than the fourth cervical of the

Vicugna; but, relatively to its width, it is much shorter and stouter than this bone in either the Guanaco or the Vicugna. There are no longitudinal ridges on the surface of the vertebra below the prezygapophyses, in which respect *M. Boliviensis* differs from *M. Patachonica*, and approaches the *Aucheniæ*. The anterior articular facet of the centrum is concave from above downwards, in consequence of the projection of the thickened and convex lower third of that face; the posterior facet is not only concave from above downwards from a similar cause, but is also concave from side to side. The concavity of both articular facets is greater than in *M. Patachonica*, and the present species departs, in these respects, more widely than the latter does from the *Aucheniæ*.

The astragalus (Plate VI. [Plate 32.] fig. 2).—This bone is, again, quite that of the Patagonian species in miniature, differing chiefly in the proportions of its dimensions, as shown by the subjoined table:—

	Macrauchenia Boliviensis.	*M. Patachonica.*	*Guanaco.*	*Vicugna.*
	in.	in.	in.	in.
Length . . .	1·45	3·3	1·6	1·3
Greatest width .	1·2	2·7	1·2	·85
Greatest depth .	·85	2·15	·95	·8

If we take the lengths of the astragali, it will be observed that their proportions in the Bolivian and Patagonian *Macraucheniæ* are not the same as those of the cervical vertebræ. The astragali bear the ratio of 1 : $2\frac{1}{3}$, while the cervical vertebræ gave 1 : $1\frac{7}{9}$. Furthermore, the proportions of length, width, and depth in the two astragali are different. Like the cervical vertebra, the astragalus of *M. Boliviensis* is a, relatively, stouter bone than that of the Vicugna; though instead of being shorter it is a little longer, occupying a position, in point of absolute length, between the astragalus of the Vicugna and that of the Guanaco. As the astragalus thus yields results agreeing very well with those given by the cervical vertebra, we may safely assume that not only the absolute size, but the proportions of the body of *Macrauchenia Boliviensis* were nearly those of the existing Llamas, and differed widely from those of the heavy and huge *Macrauchenia Patachonica*.

The tibia.—What remains of the bones of the hind leg confirms this view of the proportions of *Macrauchenia Boliviensis*. I have the proximal end of the left tibia, minus the fibula, and with the outer articular condyle broken away. Below this point, the outer edge and surface of the fragment are uninjured, and the posterior face is in good preservation, but the internal face is somewhat crushed.

The muscular ridges on the posterior face are as well marked as in the skeleton of the Guanaco, and far more distinct than in that of the Vicugna, yielding additional evidence of the adult condition of the animal, to that afforded by the absence of epiphyses.

The antero-posterior diameter of the tibia, measured from the posterior edge of the internal articular facet to the anterior edge of the crest of the tibia, is, in—

M. Boliviensis.	*M. Patachonica.*	*Guanaco.*	*Vicugna.*
in.	in.	in.	in.
2·4	5·4	2·3	2·1,

so that the depths of the proximal ends of the tibiæ of the two *Macraucheniæ* have the ratio of 1 : 2¼, which corresponds very well with the proportions of the astragali, and confirms the conclusions already arrived at, as to the relative lightness of the limbs of this species in comparison with those of *M. Patachonica*, and as to the similarity of the proportions of the Bolivian species to those of the Llamas.

What remains of the outer edge of the tibia is sufficient to prove that the fibula must have remained unanchylosed to the tibia for a much greater distance than in the Patagonian species. From the manner in which the outer tuberosity of the proximal end of the tibia is broken off, I am inclined to suspect that the fibula was anchylosed to it at this point; and perhaps, as in the *Aucheniæ*, its proximal end was represented only by a bony style.

The scapula is represented merely by a mutilated fragment, comprising the glenoid cavity and the adjacent parts. The spine of the scapula is broken off, and the glenoid cavity is somewhat distorted by the bending of one of its edges; but enough remains to show that the bone must have agreed with the scapula of *Macrauchenia Patachonica* in all essential respects, and that it therefore differed very widely from that of the *Aucheniæ*. In size, however, it nearly corresponded with the corresponding bone in the latter animal; for the greatest diameter of the glenoid cavity is 1·2 inch, the same measurement in the Vicugna being 1·0, and in the Guanaco 1·6.

The ulna.—The fragment of the ulna, consisting of part of the olecranon process and of the sigmoid cavity, is so crushed, that I can only affirm its general agreement in form with that of *Macrauchenia Patachonica*, and in size with the same bone in the Llamas.

The lumbar vertebra.—Of bones referable to this region of the body, again, there is but a single fragment, of value only so far as it

confirms the conclusions arrived at by the examination of the more perfect fossils. It corresponds very well with the posterior half of the centrum of the penultimate lumbar vertebra of *M. Patachonica* in form, and with the corresponding vertebra of *Auchenia* in size; but the crest into which the middle of its under surface is raised, and which is still sharper than that in the Patagonian species, diagnosticates it at once from any of the lumbar vertebræ of the Llamas.

The transverse diameter of the articular face is 1·1 inch, its vertical diameter 0·9. The corresponding measurements of the antepenultimate lumbar vertebra of *M. Patachonica* are 3·0 inches and 2·1; so that, as in other bones, the proportions of diverse diameters of the same bone are not the same in the two species. But as the transverse diameters of the cervical vertebræ of the two species are nearly as 1 : 3, and the transverse diameters of the lumbar vertebræ are, also, nearly in the ratio of 1 : 3, it would seem as if the different regions of the vertebral column of the two species exhibited the same proportional correspondence to one another.

The skull.—As no part of the skull of *Macrauchenia Patachonica* has yet been discovered (with perhaps the exception of part of the lower jaw), a great interest attaches to every fragment which promises to throw light upon this part of its organization; and I therefore make no apology for dwelling at some length upon the characters of the two very imperfect and mutilated portions of the cranium which turned up among the specimens submitted to me by Mr. Forbes.

The one of these (Plate VI. [Plate 32.] fig. 3) consists of rather more than half of the occipital segment of the skull, and exhibits the whole of the supra-occipital bone, with its strong occipital crest, a part of the parietal with the sagittal crest, the greater part of the right paramastoid process, and the entire right occipital condyle.

As I have already remarked, the sutures are obliterated: and this is true, not only of those which ordinarily exist between the elements of the occipital bone in young mammals, but of the lambdoidal suture, which usually persists for a longer period. The occipital foramen must, when entire, have had a depressed-oval form, the short, vertical axis of the oval being about 0·6 of an inch long. The face of the bone above it inclines upwards and forwards, at an angle of about 50° with the base of the skull, and presents a sharp ridge in the middle line, on either side of which the surface of the supra-occipital element slopes with a slight convexity outwards and forwards, at the sides and below; while, above, it becomes concave by passing almost vertically upwards in the middle line, and laterally, bending upwards

and backwards at a right angle with its previous inclination into the occipital crest.

This crest is nearly 0·2 inch thick at the sides, and becomes still thicker in the middle line, where it joins the sagittal crest. It is 1·1 inch in diameter at its widest part, and about half an inch high. Its contour is that of a parallelogram, with its angles rounded off, and the middle of its upper side rather truncated. The lateral portions project backwards rather more than its centre; so that, while, supposing the basi-occipital to be horizontal, a vertical line drawn through the posterior edge of that bone would nearly coincide with the contour of its central part, it would pass a little anterior to the plane of the lateral extremities of the crest. Inferiorly, the thick lateral portions of the crest divide into two ridges; the posterior of which turns slightly inwards and comes to an end, while the anterior, much sharper at its edge, passes forwards and outwards, and becomes continuous with the sharp ridge in which the paramastoid process terminates externally.

Behind this ridge, between the paramastoid process, the occipital condyle, and the lateral convexity of that part of the occipital bone which lies above the foramen magnum, there is a deep fossa, which is divided into two portions by a transverse ridge, extending from the outer and upper part of the condyle to the posterior and inner face of the paramastoid process. The large precondyloid foramen (probably somewhat enlarged accidentally) opens into the lower and anterior division of the fossa, beside the condyle, and about $\frac{1}{6}$th of an inch behind its anterior inferior boundary. The upper boundary of the foramen magnum is almost straight, and its summit is below the level of the superior edge of the condyle (when the base of the skull is horizontal). The condyle is divisible into an upper, smaller, obliquely ascending, and a lower, more nearly horizontal facet. The line of junction between the two, forming the posterior limit of the condyle, is rounded off and is directed obliquely outwards and upwards. The moderately convex upper facet looks upwards, backwards, and but very slightly outwards. It is broad above, where its transverse diameter amounts to nearly half an inch, and tapers off gradually to a point below and internally.

The inferior facet, less curved than the other, is 0·6 of an inch wide behind, hardly more than half that in front, and fully 0·8 of an inch long. It is slightly convex from side to side, and from behind forwards, posteriorly, where it looks downwards and outwards; convex from side to side, and slightly concave from behind forwards, in front, where it is directed more horizontally downwards. Its anterior narrow

end has a sharply defined rounded margin, which can be traced to the anterior boundary of the occipital foramen; so that the occipital condyles certainly did not coalesce in the middle line.

The paramastoid process is broken off rather above the level of the lower boundary of the occipital condyle; but, from the thinness of the fractured edge, I imagine it did not extend much further. It is broad and flattened, the direction of its greatest diameter being from behind and without, inwards and forwards. Its posterior face is directed as much inwards as backwards, and its outer margin is sharp, except towards the lower end, where it becomes rounded. Internally, it thickens before rejoining the exoccipital, in front of, and external to, the precondyloid foramen. The upper part of its anterior and external face is evidently rough and has united with the mastoid, now completely broken away; but it is difficult to say how far downwards the sutural face extended. The posterior boundary of the jugular foramen is preserved on the inner side, and in front of, the thick inner edge of the paramastoid.

The sagittal crest is continued forwards from the triangular prominence common to it and the occipital crest, and at once becomes very thin and sharp. It is broken off at a very short distance from its commencement, and at this point it is a quarter of an inch high. Its superior margin is not parallel with the contour of the middle line of the parietal region, but has a more marked upward inclination, so as to lead one to suppose that the crest rose to a considerable height in the middle of the synciput,—a conclusion which is strengthened by the great thickness of the parietals (of whose median suture no trace is visible) in the middle line. The transverse section presented by the anterior broken edges of these bones is, in fact, triangular, and the height of the triangle from its apex, which corresponds with the base of the crest, to its base (the concave inner wall of the cranium) is nearly 0·4 of an inch.

In viewing the fragment of the occiput from within, one is surprised by the great thickness of the supra-occipital region, the bone immediately above the middle of the occipital foramen being half an inch thick. A well-marked ridge, defining the interior boundary of the cerebellar fossa, is continued downwards, forwards, and outwards, from the anterior boundary of the thick roof of the occipital foramen. There is no venous canal traceable above the inner aperture of the precondyloid foramen.

If the occiput of *Macrauchenia Boliviensis* be restored by reversing the outlines of the right half (as in Pl. VI., [Plate 32.] fig. 3), thus supplying the wanting left moiety, the following measurements may

be obtained. Side by side with them I give the corresponding measurements of the skull of the Vicugna:—

	M. Boliviensis.	*Vicugna.*
	in.	in.
Transverse diameter of the occiput from the outer edge of one paramastoid to that of the other	1·9	2·25
Ditto from the outer edge of one occipital condyle to that of the other	1·5	1·5
The transverse diameter of the occipital foramen	·7	·7

It will be observed that the two series of dimensions correspond very closely, the two latter being identical, while the *Macrauchenia* appears to have had even a narrower skull than the Vicugna. In form, the occiput of *Macrauchenia* agrees better with that of the Llamas than with that of any other ungulate animal with which I have compared it.

Thus, in an old Guanaco I find an equally well-marked ridge in the middle line of the supra-occipital element; the occipital crest is equally prominent, though not so stout; the sagittal crest is as well marked, thin and sharp, and, as in *Macrauchenia*, its superior edge ascends. There is a fossa between the occipital condyle and the paramastoid, similar in form to that in *Macrauchenia*, though much shallower. The occipital condyles are very much alike; and their relation to the precondyloid foramina is the same in both cases. The paramastoid has the same proportional breadth; and its greatest diameter is, in both cases, directed from without and behind, inwards and forwards: in both cases its inner edge is peculiarly thickened. Again, the paramastoid of the *Auchenia*, like that of the fossil, is very short, its apex hardly extending below the level of the occipital condyle.

The occiput of *Macrauchenia*, on the other hand, differs from that of *Auchenia* in the much greater thickness of the supra-occipital, which in the *Macrauchenia* has fully double the thickness of the same region in an old Guanaco, whose skull is much larger—in this respect approaching the Sheep and some other Ruminants, which have this bone very thick. The supra-occipital, also, is much higher, in proportion to its width, in *Macrauchenia* than in *Auchenia*; its lateral contours are parallel, and not divergent outwards and upwards. There is nothing in the *Macrauchenia* resembling the deep notch between the supra-occipital and the base of the paramastoid, into which a part of the mastoid fits in *Auchenia*. In contour, in fact, the occiput of the *Macrauchenia* resembles that of the *Palæotherium*

more nearly than that of any other Mammal. But, on the whole, I think it must be admitted that the resemblance of the back of the skull of the *Macrauchenia* to that of *Auchenia* is sufficiently close to justify the conclusion, that the predominance of the Cameline type, so marked in the neck, was maintained in the head of the extinct Mammifer.

The fossil which remains for description (Plate VI., [Plate 32] fig. 4) consists of two fragments of the matrix (*a* and *b*), which fit together, and to which adhere certain portions of the upper jaw and palate, together with the fractured remains of three grinding-teeth and part of the alveolus of a fourth, all of the right side, and in a continuous series. The alveoli and part of the crowns of these teeth are contained in the larger fragment of matrix,—the smaller fragment fitting against the larger and the teeth which it contains, and exhibiting the impressions of the grinding surfaces of three teeth and of their inner faces, a portion of dental substance adhering to the latter, in the case of the two anterior teeth. Of the hindermost tooth nothing is left but the impression of one fang.

The impression of the grinding surface of the first tooth is nearly four-tenths of an inch long, convex from before backwards, concave internally: the outer boundary of the impression is broken away, a fragment of dental substance adhering to the posterior part of its inner face. The part of the larger portion of the matrix (*a*) which should contain the alveolus of this tooth is absent. The antero-posterior extent of the coronal impression of the second tooth is a little more than 0·4 of an inch; it is concave from before backwards externally, nearly flat internally, and shelves with a slight convexity upwards and inwards. The inner boundary of the impression is, as in the preceding case, markedly concave; and a much larger fragment of tooth-substance adheres to it. The outer boundary of the impression is broken away, but much more in front than behind, where its width is fully 0·4 of an inch. The impressed line which separates this impression from the next is convex forwards. Corresponding with this impression there are, in the larger fragment of matrix, an almost entire conical posterior fang, about 0·4 of an inch long, lodged in a complete bony alveolus, whose outer wall is broken away, and the posterior half of a similar alveolus for an anterior fang: there is no trace of a third alveolus or fang; and, indeed, there seems to be no room for one. The fang which exists is connected below with a portion of the crown; but this is so broken, that all that can be remarked of it is its marked internal convexity.

The coronal impression of the third tooth is half an inch long;

like the preceding, its face shelves upwards and inwards. The posterior part of its outer margin is broken away; but it is clear that this crown was quite as wide as that which preceded it, if not wider; the surface appears, however, to have been more evenly flat. The inner perpendicular face of the impression presents two concavities, separated by a slight ridge.

More of this tooth is preserved than of any other; the outer wall of the maxilla is, for the most part, preserved over it, and encloses the alveoli of two external fangs. There is evidently at least one, and perhaps two, internal fangs. The whole thickness of the inner and posterior part of the crown is preserved, and the posterior and inner half of its worn face; the rest of the tooth is broken away. The posterior and outer fang, partially exposed, is 0·3 of an inch long, conical, and slightly inclined backwards, as well as upwards and inwards. The crown, where it joins the fang, is 0·4 of an inch long; so that it must have widened a little below. The vertical height of the crown of the tooth posteriorly and internally is hardly more than 0·15; anteriorly and internally it is broken; but, when entire, it had a height of at least 0·2. The inner surface of the tooth is divided into two tolerably well-marked subcylindrical faces, which correspond with the impressions on the inner wall of the coronal impressions.

The outer moiety of the crown is altogether broken away; the inner moiety, broken anteriorly, exhibits in its posterior half a smoothly worn facet, concave from before backwards, and inclined not only downwards but slightly backwards. A narrow fringe of enamel appears to surround the worn dentine of this face, which is wider in the middle than at the two ends. The true outer face of the enamel can be traced from the inner face of the tooth, continuously, round the posterior boundary of this worn facet, and as far as its most dilated portion on the inner side. It is concave outwards, and presents a slight inflexion midway between the posterior end of the facet and its middle dilatation. Beyond the dilated middle of the facet, its enamel-wall seems to have been united with that of the opposite half of the tooth; but it is traceable forwards, becoming concave externally, past the anterior end of the worn facet, to the anterior margin of the tooth, where it bends round, and again becomes continuous with the enamel of the inner face.

This tooth, therefore, appears to have possessed an internal division, elongated from before backwards, surrounded by a narrow band of enamel—having its inner contour produced into two convexities, separated by a slight vertical depression, while its outer wall presents two concavities, separated by a slight ridge which lies rather

behind the level of the depression on the inner face. By use, the posterior part of this division wore down into a facet, concave from before backwards, and separated, by a transverse ridge, from the facet in front of it. A longitudinal fossa separated the posterior moiety, at least, of this division of the tooth, from the outer division.

Imperfect as is this fragmentary grinder, certain important conclusions may, I conceive, be very safely drawn from its structure. The predominance of the longitudinal, to the exclusion of transverse valleys and ridges in the crown of the tooth, the distinct, though not strongly marked, crescentic form of the internal division of the tooth, and its short crown, remove it from the teeth of any known Perissodactyle Mammal, and lead one, at once, to seek its analogue among the *Artiodactyla*; and of these the Ruminants alone, so far as I know, offer anything like it. The inner grinding-surface of any true molar of a Ruminant, however, exhibits two ridges and three depressions, while that of the *Macrauchenia* has only one ridge, with a concave shelving depression behind, and doubtless, in the perfect condition, another in front; in other words, it has the contour exhibited by one of the hinder premolars of a Ruminant. The inner division of a posterior premolar of *Auchenia* has its convex inner surface undivided by any vertical depression; and its outer posterior margin exhibits no marked inflexion: but such an inflexion exists in the corresponding teeth of the Giraffe and of many Deer, in some of which latter a vertical groove, dividing the inner face into two convexities, may also be noted.

I am of opinion, therefore, that the tooth in question is a posterior premolar, and that it was constructed upon the Ruminant type. In this case, however, the dentition of *Macrauchenia* must have departed widely from that of the *Camelidæ*; for there were certainly two teeth with flat grinding crowns in front of that just described, which would give, at least, three premolars in all, or as many as are found in ordinary Ruminants.

I am strengthened in the conviction that there were as many as three premolars, by the rest of the structure of this interesting fragment. Within the series of teeth just described, in fact, it presents a considerable portion of the roof of the palate, some of whose bony matter remains. At a distance of half an inch from the inner wall of the posterior premolar, a longitudinal sutural line traverses the whole length of the palatine surface, and ends abruptly (in consequence of the fracture of the matrix) as well behind as in front. Its posterior end is 1·2 of an inch behind a transverse line drawn at the level of the posterior margin of the last premolar. Opposite and

behind this tooth, the right half of the palate is marked by what might hastily be taken for a suture, but which is nothing but a fracture. Behind it, and 0·9 of an inch in front of the posterior end of the longitudinal suture, two curved transverse lines, convex forwards, which I believe to be the maxillo-palatine sutures, pass into the longitudinal suture.

Thus, it is clear that the palate must have extended back for 1·2 of an inch behind the third grinding-tooth.

Supposing this tooth to have been succeeded by three others whose length, if they were molars, would be probably between 0·6 and 0·7 of an inch, it follows that the posterior margin of the palate must have extended, at least, as far back as the posterior margin of the second molar. This is further than it extends in the *Auchenia* (the very forward extension of whose palatine aperture is exceptional among the *Artiodactyla*), but it is not so far as in the Camel, where the posterior boundary of the palate is opposite the middle of the last molar.[1]

This backward extension of the palate is, so far as it goes, in favour of the view to which the consideration of the dentition and the structure of the occiput leads, viz., that the cranium of the *Macrauchenia* was constructed upon an essentially Artiodactyle type.

The following are the dimensions of the palate and teeth of *Macrauchenia Boliviensis*, and those of the corresponding parts in the Vicugna:—

		Macrauchenia.	*Vicugna.*
Width of palate inside the grinding teeth[2]	about	1·0	1·25 (at widest).
Antero-posterior length of four grinders . .	more than 2·0 less than 2·5		2·2

[1] The attempt to differentiate the *Artiodactyla* and *Perissodactyla* absolutely by the position of the posterior margin of the bony palate is fallacious. On an average it is doubtless true that the bony palate extends further back in the former than in the latter; but the bony palate extends to a line joining the anterior edges of the last molars in *Hyrax*; while in the full-grown Guanaco, a similar line is 0·4 of an inch behind the posterior boundary of the palate.

[2] The six grinding-teeth of the lower jaw, which Professor Owen has provisionally referred to *Macrauchenia* (British Association Reports, 1846), are said to form a series 9 inches long. A series of six such teeth of the lower jaw of *Macrauchenia Boliviensis* could not have exceeded 4 inches in length, and was probably shorter. Under these circumstances, the heads (as measured by the teeth) of the two species would be in nearly the same proportion as their astragali, and in very different proportions from their cervical vertebræ. This is not improbable; for the Vicugna has a much lighter head than the Guanaco, if the cervical vertebræ be taken as the standard. The length of the fourth cervical of the Vicugna is to that of the same bone in the Guanaco as 1 : 1⅐, while the length of the head in the two is as 1 : 1½.

The narrower palate of the *Macrauchenia* agrees with its narrower occiput, while it exhibits the same general correspondence with the Vicugna as has been met with in the limbs and vertebræ.

Thus I conceive that an attentive examination of these scanty remains is sufficient to prove that, when they were embedded, there lived in the highlands of Bolivia a species of *Macrauchenia* not half as large as the Patagonian form, and having proportions nearly as slender as those of the Vicugna, with even a lighter head; and it is very interesting to observe that, during that probably post-pleistocene epoch, a small and a large species of more or less Auchenoid Mammal ranged the mountains and the plains of South America respectively, just as at present the small Vicugna is found in the highlands, and the large Guanaco in the plains of the same continent.[1]

The structure and geological date of the genus *Macrauchenia* may serve, if taken together, to point an important palæontological moral. Professor Owen, in the able memoir cited above, has clearly pointed out the remarkable combination of Artiodactyle and Perissodactyle characters exhibited by *Macrauchenia*, which unites the eminently characteristic cervical vertebræ of the Artiodactyle *Camelidæ* with the three-toed fore foot and the triply trochantered femur of the *Perissodactyla*; and with an astragalus which, in the apparent entire absence of any facet for the cuboid, is, I may affirm, more Perissodactyle than that of any member of the order, except *Hyrax*.

None of the older Tertiary mammalia can produce such strong claims to be considered an example of what has been termed "a generalized type" as *Macrauchenia*; and yet there seems little doubt that the latter is the South American equivalent, in point of age, of our Irish Elk!

Again, *Macrauchenia*, alone, affords a sufficient refutation of the doctrine that an extinct animal can be safely and certainly restored if we know a single important bone or tooth. If, up to this time, the cervical vertebræ of *Macrauchenia* only had been known, palæontologists would have been justified by all the canons of comparative anatomy in concluding that the rest of its organization was Camelidan. With our present knowledge (leaving *Macrauchenia* aside), a cervical vertebra with elongated centrum, flattened articular ends, an internal vertebral canal, and imperforate transverse processes, as definitely characterizes one of the Camel tribe as the marsupial bones do a Marsupial—and, indeed, better; for we know of recent non-marsupial animals with marsupial bones. Had, therefore, a block containing an

[1] As the Guanaco ranges into the highlands, it may not be a too sanguine expectation to hope for the future discovery of remains of the great *Macrauchenia*, also, in Bolivia.

entire skeleton of *Macrauchenia*, but showing only these portions of one of the cervical vertebræ, been placed before an anatomist, he would have been as fully justified in predicting cannon-bones, bi-trochanterian femora, and astragalia with two, subequal scapho-cuboidal facets, as Cuvier was in reasoning from the inflected angle of the jaw to the marsupial bones of his famous Opossum. But, for all that, our hypothetical anatomist would have been wrong; and, instead of finding what he sought, he would have learned a lesson of caution, of great service to his future progress.

EXPLANATION OF PLATE VI. [PLATE 32.].

Fig. 1. Cervical vertebra of *Macrauchenia Boliviensis*, Huxley; restored from the opposite side, posteriorly.

Fig. 1 *a*. The same vertebra, viewed from in front.

Fig. 1 *b*. The same vertebra, viewed from behind.

Fig. 2. Astragalus (left), from above.

Fig. 2 *a*. ,, ,, from below.

Fig. 2 *b*. ,, ,, from the outer side.

Fig. 3. Fragment of the occipital portion of the cranium, restored in outline.

Fig. 3 *a*. The same fragment, viewed from without and laterally.

Fig. 4. Part of the upper jaw and palate, and lateral view (*a*) of the crown of the most perfect tooth.

Fig. 4 *a*. Side-view of the large fragment of the matrix containing the teeth, with the smaller fragment, exhibiting the coronal impressions, adapted to it.

[PLATE 32.]

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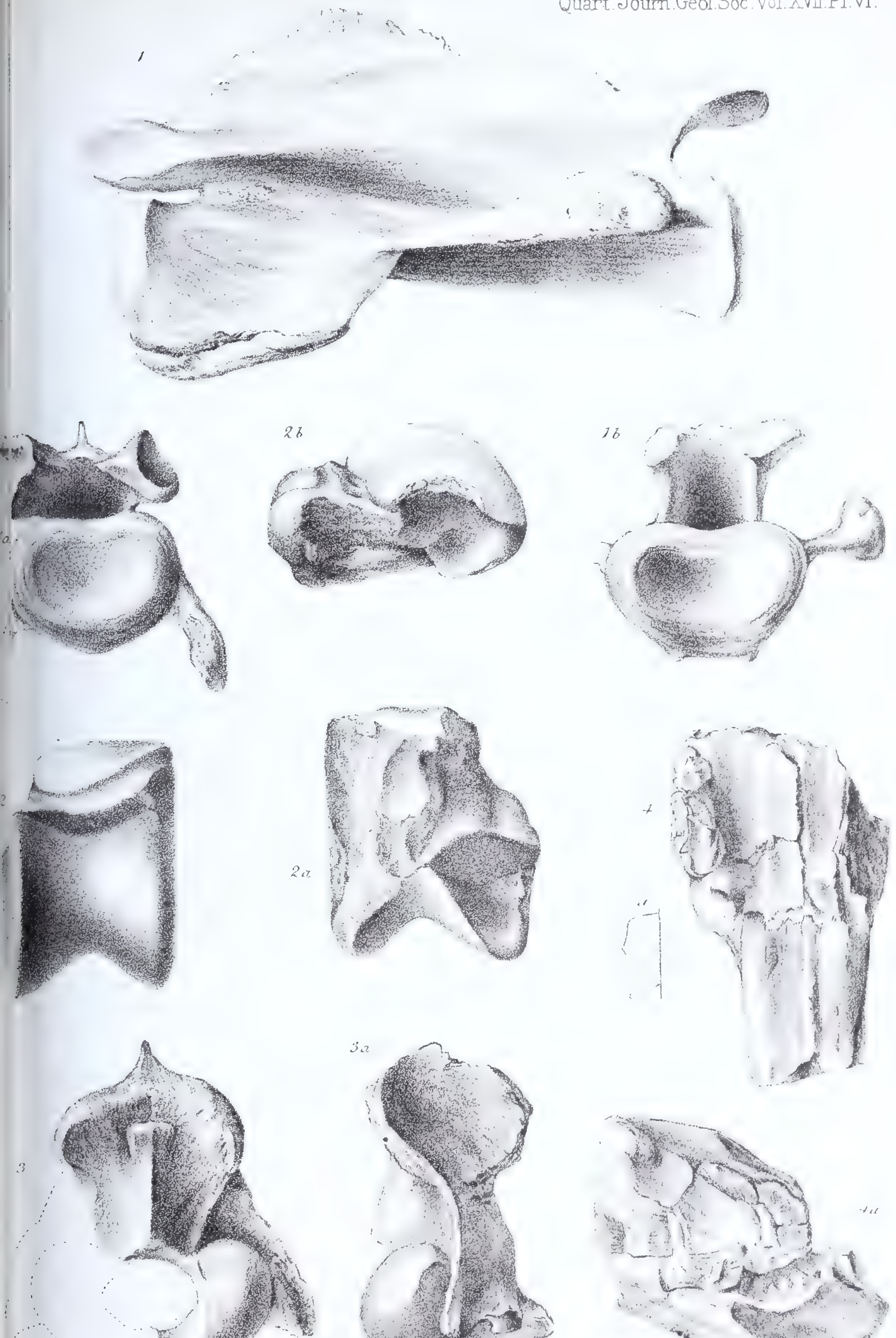

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MACRAUCHENIA BOLIVIENSIS.

XXII

ON PTERASPIS DUNENSIS (ARCHÆOTEUTHIS DUNENSIS, *ROEMER*).

Quarterly Journal of the Geological Society of London, vol. xvii., 1861, *pp.* 163—166. (*Read January* 23, 1861.)

THE fourth volume[1] of the 'Palæontographica' of Dunker and Von Meyer (1856) contains a memoir on "*Palæoteuthis*, a genus of Naked *Cephalopoda* from the Devonian rocks of the Eifel," by the well-known paleontologist, Dr. Ferd. Roemer. The fossil upon which this genus is founded is described as an oval, convex, symmetrical, shield-like body, marked by two diverging longitudinal elevations or keels, and exhibiting on its surface a peculiar ornamentation, consisting of curved parallel ridges, so fine that there are as many as 8 or 10 to a line. All traces of any deeper layer than that which exhibits these ridges had disappeared. In discussing the affinities of this fossil, Dr. Roemer decides in favour of its being the internal shell of a Naked Cephalopod, upon the grounds, first, of its general form, and, secondly, of the presence of the diverging keels, in both of which respects he considers the fossil to resemble the internal shell of a *Sepia*. And he adds: "Inasmuch as the fine superficial sculpture is altogether peculiar and different from that of the cuttle-bone, and since, further, the fact that the fossil exhibits such a structure only upon its surface leads one to suspect that it was not a thick ossicle, but thin and horny like that of *Loligo*, and since, finally, its occurrence in so old a formation makes its generic identity with the living genus improbable, it will be justifiable to consider the fossil as the type of a new genus, although its clear definition can only be rendered possible by the discovery of more perfect specimens, and perhaps of other parts of the animal" (p. 74).

[1] Page 72, plate 13.

Dr. Roemer then remarks on the evidence thus furnished of the occurrence of naked *Cephalopoda* at an earlier period than had hitherto been supposed; and, in a note, he refers to Dr. Kner's paper on *Cephalaspis Lloydii* and *C. Lewisii*, disputing the conclusion at which Kner had arrived, that these fossils are remains of Naked Cephalopods, and affirming "that the structure of the shell of these disks is rather that of *Crustacea*, and that their whole external form leads to the supposition that they are allied to such palæozoic *Crustacea* as *Dithyrocaris* or *Pterygotus*." Carefully executed figures accompany the memoir from which these citations are made.

In Leonhard and Bronn's 'Jahrbuch' for 1858, p. 55, Professor Roemer returns to this subject, in a short "Notice of a second specimen of *Archæoteuthis*[1] *Dunensis*, from the clay-slates of Wassenach, on the Laacher-See," in which specimen the internal structure of the shell is preserved.

"The form and size of this specimen," says Professor Roemer, "agree essentially with those of the first specimen. Like the latter, it is imperfect, the lower end being absent. The fossil is a coal-black, brittle, horny substance, sharply defined against the slaty grey of the matrix; the thickness of the layer which it forms is about $\frac{2}{3}$rds of a line, as can be distinctly seen by the transversely fractured circumference. The sculpture of the surface is to be observed only over a small space. Here it exhibits the same fine lines as the Daun specimen. For by far the greater part of its extent, the superficial layer of the shell is destroyed, and the internal structure is revealed so distinctly as to make this specimen particularly remarkable. It consists of small prismatic cells, disposed perpendicularly to the surface of the shell. The transverse section of the cells is irregularly hexagonal, or even polygonal; the diameter of the cells is such, that three or four occur in the space of a line, whence the separate cells are perfectly recognizable with the naked eye. The depth of the cells is equal to about one-third of the thickness of the shell. The lowermost layer of the shell appears not to take part in this coarsely cellular structure, but to be much more compact.

"If this structure be compared with that of the shell of *Sepia officinalis*, L., the close analogy of the two is obvious. Only, in the living genus the cells are much finer and are disposed in numerous thin layers one over the other, whilst in the fossil species but a single such layer is discernible. In any case, this cellular structure of the

[1] In Bronn and Roemer's 'Lethæa Geognostica,' vol. i. p. 520, the name *Palæoteuthis*, having already been employed by D'Orbigny, is given up, and *Archæoteuthis* substituted for it.

fossil shell indicates its affinity rather with *Sepia* than with *Loligo*, as I had previously supposed."

The specimen from Wassenach thus described has now passed into the collection of the British Museum; and my friend Mr. Woodward (who had already divined the precise nature of the so-called *Palæoteuthis* in a note to p. 417 of his 'Manual of the Mollusca') having called my attention to the specimen, without giving me any informa-

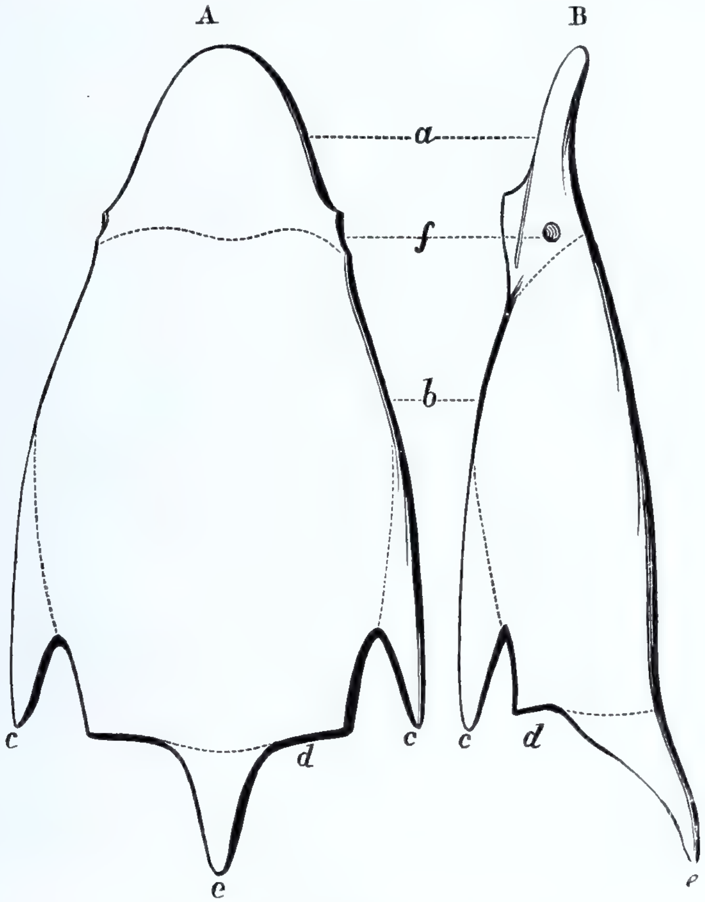

DIAGRAM OF A RESTORED PTERASPIS.

a. Snout or rostrum, united with *b*, the shield-like disk. *c*. The cornua of the latter; *d*, its median backward prolongation; *e*, the median posterior spine into which the last is produced. *f*. Orbits or nasal apertures.

tion as to its previous history, I at once affirmed it to be a *Pteraspis*,—being led to this determination by the eminently characteristic striation of the outer surface, combined with the no less peculiar polygonal cells of the middle layer.[1] There is nothing like either

[1] I have carefully described these structures in my memoir "On *Cephalaspis* and *Pteraspis*," Quarterly Journal of the Geological Society, 1858, vol. xiv.

of these tissues in any Cephalopod or Crustacean with which I am acquainted—the construction of the cuttle-bone being totally different; and they exist, in combination, in no animal structure which has yet been described, except *Pteraspis*. In form, and in the presence of the diverging ridges described by Professor Roemer, the fossil perfectly agrees with many of our English *Pteraspides*; and I have therefore no hesitation in expressing the opinion that *Archæoteuthis* must disappear from the list of Dibranchiate Cephalopods, and consequently that the palæontological history of this group cannot, at present, be traced back further than the beginning of the Mesozoic epoch.

The distinction of species among the *Pteraspides* is a difficult matter; and, pending investigations which I have been for a long time making on this subject, I leave open the question whether Professor Roemer's specimens are or are not types of a new species, which, in the latter case, must be termed *Pteraspis Dunensis*.

In conclusion, I may remark that, as I have already pointed out elsewhere (British Association Reports, 1858), the test of *Pteraspis*, as commonly met with, consists of only a part of the cephalic shield of that singular fish, the whole shield being not a little similar to that of *Cephalaspis*. In *Pteraspis rostratus*, for example, the entire shield has the form indicated by the subjoined outlines, of which A represents a dorsal, and B a lateral view. It consists of a cephalic rostrum (*a*), more or less elongated and pointed according to the species, passing posteriorly into the broad shield (*b*), which (as the dotted lines indicate) is commonly found broken off and alone. When perfect, this is produced laterally and posteriorly into two cornua (*c*), and in the middle line behind passes into a broad prolongation (*d*), which gives rise interiorly to a long, curved, and backwardly produced spine (*e*). Upon each side of the test, where the rostrum joins the rest of the shield, there is a round, well-defined aperture (*f*), which may be either the orbit or the nasal aperture.

It is not easy to find an exact parallel for such a cephalic covering as this among existing fishes. *Loricaria*, *Tetrodon naritus*, *Acipenser*, and *Spatularia* seem to present the nearest analogies—the two former being much more remote than the two latter. In fact, if the bony cephalic shield of the Acipenseroid fishes were ossified in one piece, it would very closely resemble that of both *Cephalaspis* and *Pteraspis*, and would hardly differ more from either than the two from one another.

XXIII

Decade the Tenth

PRELIMINARY ESSAY UPON THE SYSTEMATIC ARRANGEMENT OF THE FISHES OF THE DEVONIAN EPOCH

Memoirs of the Geological Survey of the United Kingdom. Figures and Descriptions illustrative of British Organic Remains. 1861.

THE endeavour to determine the systematic position of *Glyptolæmus*, a genus of Devonian fishes, first described and figured in Dr. Anderson's interesting work upon "Dura Den,"[1] and more fully discussed and illustrated in the course of the present Decade, has gradually led me to reconsider the whole question of the classification of the fishes of this epoch and, eventually, to arrive at results which seem to necessitate an important modification of the received arrangement of the great order of Ganoidei.

I propose, in the course of the pages of this preliminary essay, to take the reader through the various steps of the argument which terminates in this conclusion; and, commencing with a brief enumeration of the most important characters of *Glyptolæmus*, I shall proceed to the discussion of the peculiarities of other genera, more or less nearly allied to it, with the view of demonstrating, finally, that *Glyptolæmus* is a tolerably typical member of a large and well defined family of Ganoids, which abounded in the Devonian epoch, but whose members have been less and less numerous in more modern formations, until, at present, its sole representative is the African *Polypterus*.

Glyptolæmus Kinnairdi (fig. 1, and Plates I. and II.) [Plates 33. 34[2]]

[1] Dura Den; a Monograph of the Yellow Sandstone, and its remarkable Fossil Remains. 1859. [2] These two plates come in the following paper on "Glyptolæmus Kinnairdi."

the only known species of its genus, is a fish with an elongated body, a depressed head and a conically tapering caudal extremity. The orbits are situated forwards, while the gape extends far back. The frontal

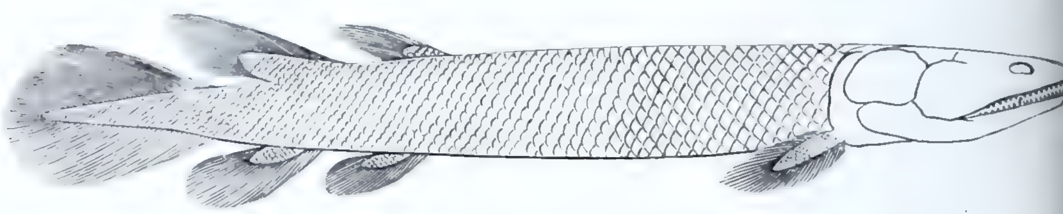

Fig. 1. Restoration of *Glyptolæmus.*

bones (fig. 2) are distinct from one another and from the parietals, which last are not shorter than the frontals, and, though in contact throughout the whole length of their inner margins, are perfectly distinct from one another. Three bones, or scales (for they seem to partake as much of the nature of the latter as of the former), a median and two lateral, roof in the occipital region. The middle of the jugular

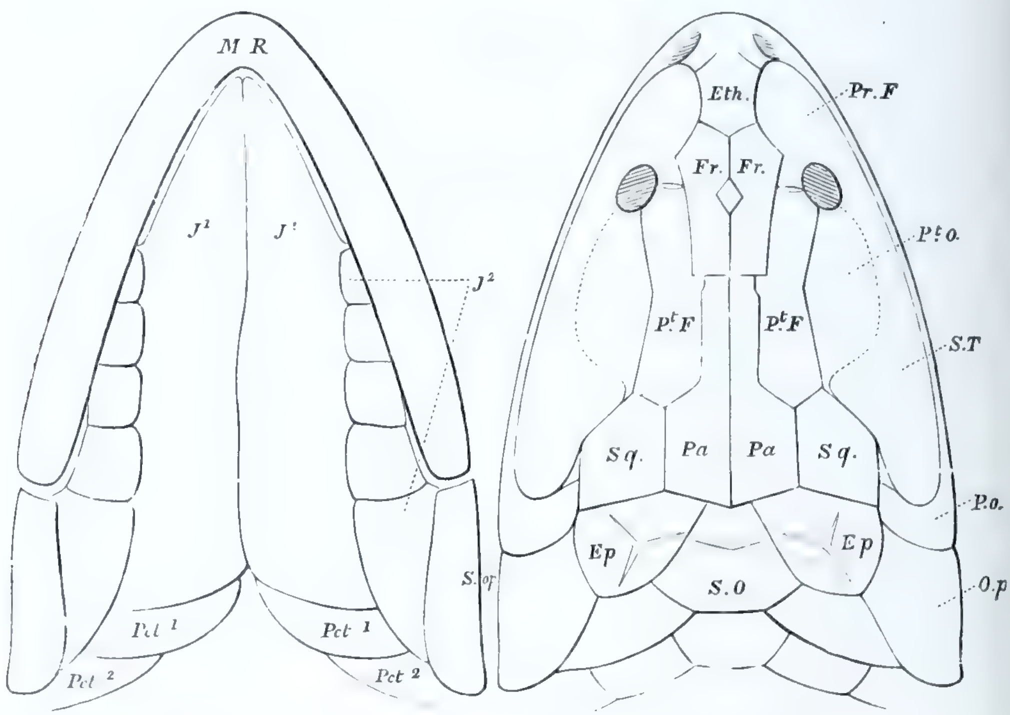

Fig. 2. Diagram of the Head of *Glyptolæmus.*—For an explanation of the letters, see p. 460.

region, or that comprised between the two rami of the mandible upon the under surface of the cranium, is occupied by two large, triangular, squamiform, bones—the *principal jugular plates* (J^1);

while the interval left between them and the mandibular rami, on each side, is taken up by a series of smaller, quadrate plates, which increase in size from before backwards—the *lateral jugular plates* (J^2) There is no rhomboidal *median jugular plate* interposed between the anterior part of the inner edges of the principal jugular plates. The teeth are of two kinds; smaller, set in a close series along the edges of the jaws; and larger, placed at intervals along the palate, and perhaps along the inner side of the mandible. The larger teeth have grooved bases, and appear to be composed of dendrodentine.[1]

The pectoral arch is covered by two triangular, sculptured, osseous plates (Pct^1, Pct^2), which meet in the middle line below and are superficial to the so-called coracoids. The paired, or pectoral and ventral, fins are lobate; that is, the fin has a central axis, or stem, covered with scales. There are two dorsal fins, placed in the posterior half of the body. The ventral fins are situated under the first dorsal, and are succeeded by a single anal. The caudal fin, whose contour is rhomboidal, is divided into two equal lobes by the prolonged conical termination of the body; in other words, the fish is diphycercal, or truly homocercal.[2]

Every ichthyologist will admit the singularity of this combination of characters, but a careful analysis of the structural peculiarities presented by other fossil fishes of the same age, will show, that, so far from isolating *Glyptolæmus*, they closely unite it with several other genera.

That genus which appears to me to approach it most closely is the *Gyroptychius* of M'Coy, whose structure has received admirable elucidation from Professor Pander in his beautiful monograph "Ueber die Saurodipterinen, Dendrodonten, Glyptolepiden und Cheirolepiden des Devonischen Systems" (1860), to which I may refer those who desire to obtain a more particular acquaintance with the details of its organization.

Here I must content myself with reproducing in a reduced woodcut (fig. 3) Professor Pander's restoration of the fish, which may be compared with the restored woodcut of *Glyptolæmus* (fig. 1)

[1] Prof. Pander applies the term "Dendrodonts" to those fishes the pulp cavities of whose teeth appear branched, in consequence of the folding of their walls; and such folded dentine may be conveniently termed "dendrodentine."

[2] I have endeavoured to show elsewhere (Quarterly Journal of Microscopical Science, Oct. 1858) that the so-called "homocercal" *Teleostei* of the present epoch are in reality excessively heterocercal; but the word "homocercal" is now so generally understood to signify a tail like that of most existing *Teleostei*, that I prefer to employ Prof. M'Coy's term "diphycercal" for truly homocercal tails. See, on this point, Kölliker, "Ueber das Ende der Wirbelsäule der Ganoiden, 1860," and Van Beneden, "Sur le Développement de la Queue des Poissons Plagiostomes," Bull. de l'Acad. Royale Belgique, 1861.

and with the Plates, and with stating that the head, the body, and the fins of *Gyroptychius* might be described in the terms which have just been applied to *Glyptolæmus*. Pander, however, makes no mention of lateral jugular plates; the scales, which are as often

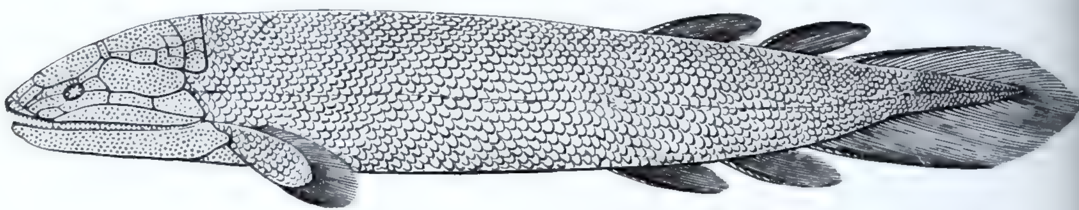

Fig. 3. Restoration of *Gyroptychius* (after Pander).

oval as rhomboidal, are sculptured in a very different manner from those of *Glyptolæmus*, and, according to Pander, the anterior edges of the median fins are provided with fulcra.

Glyptopomus (Agassiz) is another genus whose close alliance with *Glyptolæmus* is evidenced by the structure of its skull, of which there is a fine specimen in the British Museum. It is very depressed and has two distinct frontal bones, separated anteriorly by a small rhomboidal plate; there are two long and distinct parietals, and

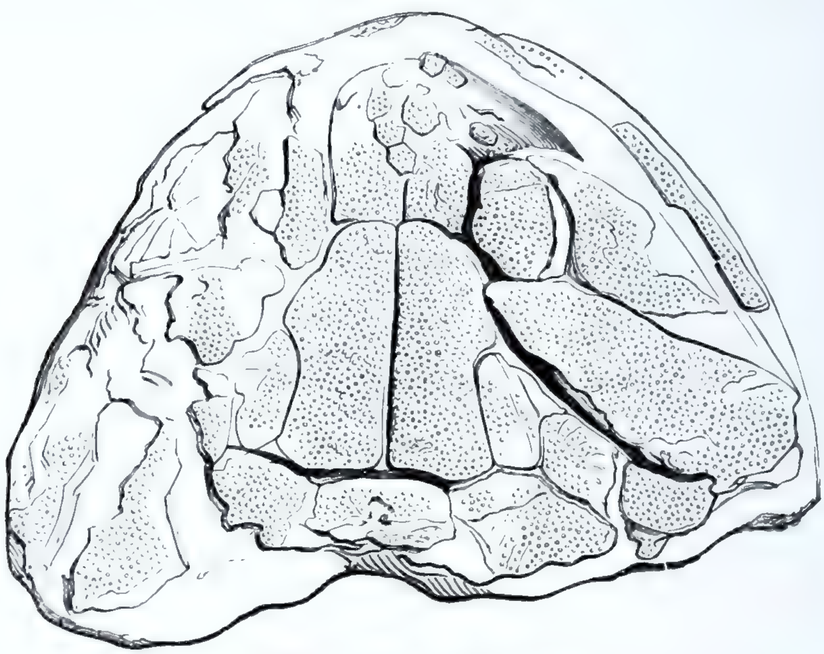

Fig. 4. Head of *Glyptopomus*.

three bones, one median and two lateral, behind these, covering the occiput. The orbits are situated far forward, the gape is greatly elongated, there are two principal jugular plates, and the pectoral arch is as in *Glyptolæmus*. A fine specimen in the Museum of

Practical Geology shows that some of the teeth, at any rate, were of large size, and longitudinally grooved at their bases.

Only three specimens of *Glyptopomus* are at present known, and no one of these exhibits either the paired or the median fins; but the close correspondence of the cranial structure of this genus with that exhibited by *Glyptolæmus*, leaves no doubt on my mind that, when discovered, the fins will be found to be similar, in all essential respects, to those of the latter genus (*see* note, p. 460). The sharply rhomboidal scales are thicker in proportion than those of any other Devonian fish, and are pitted upon their surfaces like the scutes of the Crocodilia.

As has been seen, the angles of the scales of *Gyroptychius* are apt to become rounded off, so as to present a transition from the rhomboid to the cycloid contour, and, hence, it is less surprising than it seems at first sight, to find fishes with eminently cycloid scales, so similar, in all the essential features of their organization, to *Glyptolæmus*, *Gyroptychius*, and *Glyptopomus*, as imperatively to demand a place near them in any natural arrangement.

Holoptychius (Agassiz), for example, has a depressed head (though deeper than that of *Glyptolæmus*), and a conically tapering caudal extremity; the orbits are situated far forwards and the gape extends far back. The frontal bones are distinct from one another, and from the parietals, which last are large and co-adapted, though quite distinct; the occiput is covered in by three bones, a median and two lateral; there are two principal and a number of lateral jugular plates, and there is no rhomboidal median jugular plate interposed between the principal jugulars. Some of the teeth are larger than the others, and longitudinally striated at their bases. The paired fins are very acutely lobate, and there are two dorsal fins placed in the posterior half of the body. The ventral fins are situated under the first dorsal, and are succeeded by a single anal.

Thus far, the reader who compares this description with that of *Glyptolæmus* already given, will find the two essentially identical. But the tail of *Holoptychius* differs from that of *Glyptolæmus*, in that it is little more than semi-rhomboidal, the upper moiety being far less developed than the lower,[1] and the scales are,

[1] In my restoration of *Holoptychius* (Dr. Anderson's "Dura Den," p. 69) I have represented the fish with a diphycercal tail; but I am now prepared to admit that the evidence on which I rested this conclusion was not trustworthy, and that Sir Philip Egerton's view of the case is in all probability correct. However, I must say, that I have never yet seen a *Holoptychius* with its caudal extremity in a perfectly satisfactory state of preservation.

in form and sculpture, widely different from those of the latter genus.

That *Platygnathus* (Agassiz), if we restrict the name to the fish whose caudal extremity is figured by Agassiz ("Vieux Grès Rouge," Tab. 25), is very closely allied to *Holoptychius* cannot be doubted; indeed, the only serious question regarding it, in the absence of further materials for its reconstruction, seems to be, whether it should really form a separate genus; so that I may pass on to another generic type, *Glyptolepis* (Agassiz).

This genus is briefly mentioned in the "Recherches sur les Poissons Fossiles," ii. p. 179, but Agassiz first described and figured species of

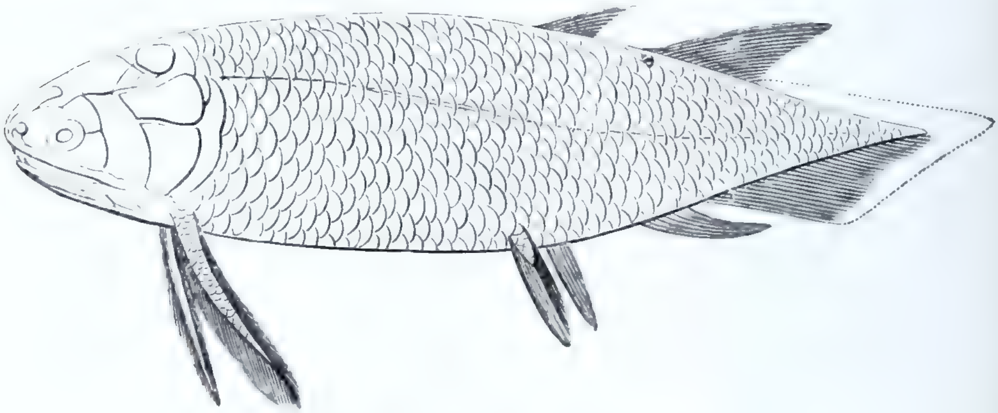

Fig. 5. Restoration of *Holoptychius.*

it in the "Monographie des Poissons du Vieux Grès Rouge," p. 62, where *Glyptolepis* heads the family of the "Célacanthes," and is said to comprise fishes of moderate size, with pyriform bodies, and with heads which are small, short, flattened, and have an almost semicircular contour. The rami of the mandible are stated to be beset throughout their length with a single series of small, equal, conical teeth, which seem to approach those of *Dendrodus* and *Holoptychius* in structure, and to have a dendritic pulp cavity surrounded by folded dentinal walls. *Glyptolepis microlepidotus*, however, is said (p. 65) to possess large teeth alternating with small ones in the lower jaw. The upper jaw projected beyond the lower a little, and had similar teeth. The throat was provided, as "in all ancient "Cœlacanths and in *Polypterus*, with two mobile triangular plates, "which replace the branchiostegal rays."

The scales were delicate, rounded, and so much imbricated that the anterior one sometimes covered more than half of its successor. Their upper faces were entirely smooth, and covered with a delicate layer of enamel, which, apart from some concentric lines of growth,

exhibited no ornamentation. Their inferior faces were also smooth, and formed by a very delicate layer of bone. The mass of the scale was formed by an osseous and spongy substance, adorned with fine rays, which radiated from the centre of the scale. These rays were intersected by concentric and circular lines, so that a scale, whose smooth layer is worn away, presents a number of small, elongated cells, disposed in circular series, almost like the seats of an amphitheatre.

In the "Additions et Corrections," (l. c., p. 140), Agassiz adds a description of the scales of *Glyptolepis elegans*, which supplies an important correction to that just given. Referring to Tab. 21*a* he says, "The figure 2 a represents a scale of its natural size, and "fig. 2 the same magnified. *The folds of the surface which con-"stitute the ornaments of the visible portion of the scale* are more "distant than in the foregoing species." Thus it is admitted that *Glyptolepis* has not smooth, but sculptured scales, as, indeed, the name of the genus implies.

Agassiz enumerates a caudal, two dorsal, and two anal fins, but states that the existence of pectorals is doubtful, and that, in any case, they must have been small and inconsiderable. The ventral fins, on the other hand, are said to possess a singular structure, "which is also to be found in *Megalichthys*." A series of plates extends as a pointed band along the belly, and, becoming free at its posterior extremity, carries numerous rays on both sides, and thus forms a ventral fin, which, from the manner in which its rays are disposed, is very like an eel's tail. (Tab. 21, fig. 2.) I have examined the specimen here referred to, which forms a part of Sir Philip Egerton's collection, and, with Professor Pander, I feel satisfied that the fin in question is the very long, acutely lobate, pectoral, bent back in such a manner, that the proximal half of its posterior edge is covered by the lower margin of the abdomen of the fish.

Professor Agassiz goes on to say that the two dorsals are opposed to the two anals, and are situated so far back that the caudal directly follows them. They are so close together that the last ray of the first touches the first ray of the second. The second dorsal and anal are higher than the first, and the caudal is large, heterocercal, and triangular, appearing to be almost vertically truncated; its superior division bears numerous little fulcra.

Hugh Miller ("Old Red Sandstone," 1841,) made some important improvements upon Agassiz' description and definition of *Glyptolepis*. He pointed out with great justice (and figured a specimen demonstrating the fact), that there is only one anal, the second, or posterior

of Agassiz; the ventrals having been mistaken for an anterior anal, and he describes and gives a sketch of the sculptured outer surface of the scales.

Professor Pander, in the Monograph already cited, has carried the work of rectification still further, though even he ventures upon no restoration of *Glyptolepis*, seeming to be unacquainted with the figure of the body of the fish, from a specimen more complete than any of those of Agassiz, or of his own, given by Hugh Miller.

In addition to what was already known, he states that the principal jugular plates are separated, anteriorly, by a small rhomboidal one, and he makes the observation that "these plates, which among "living fishes occur double only in *Polypterus*, and are among fossils "known only in *Osteolepis*, *Diplopterus*, *Megalichthys*, and *Gyroptychius*, lead to the supposition that the composition of the cranial "and facial bones will differ in no important respect from what is "found in them;" and this supposition is, he states, confirmed by the similarity of the upper and lower jaws and teeth. Behind the jugular plates, and applied to their hinder edges, Professor Pander finds two others, which meet in the middle line, and resemble those which lie upon the under surface of the pectoral arch in *Polypterus*.

The scales are, in general, rounded, sometimes circular, sometimes oval, sometimes more or less quadrate, by reason of the less rounding off of their angles. They overlap in different degrees, and their external sculpture is different in different parts of the body, whence arises such an amount of unlikeness, that different species might readily be founded on scales from different regions.

The sculptured surface presents two divisions, one, more anterior, exhibits small tubercles with projecting points, which are convex posteriorly, concave anteriorly, and are disposed in regular series converging towards a central point, which, however, they do not reach.

The posterior segment is covered with wavy longitudinal costæ, which gradually diminish in thickness from the anterior towards the posterior edge.

Professor Pander gives a figure of this peculiar sculpture, a woodcut copy of which I subjoin, and side by side with it a careful drawing of the sculpture of the scale of a *Glyptolepis* from Wick, in an even better state of preservation.

There can be no doubt that the scales of *Glyptolepis* possess the ornamentation here represented. Not only does Professor Pander positively state that the scale figured by him was worked out from a Lethen Bar nodule, and formed part of the unquestionable

Glyptolepis represented in his Plate 7, fig. 4; but the specimen of *Glyptolepis leptopterus* represented by Agassiz in the "Vieux Grès Rouge," Tab. 21, fig. 2, and now in Sir Philip Egerton's collection, has obviously sculptured scales and cranial bones. And I find that by scraping away the inner layers of the scales of undoubted examples of this genus, in the Museum of Practical Geology and in that of the Royal College of Surgeons, the points and ridges of the sculpture remaining imbedded in the rock are easily displayed. The clear recognition of the fact that this elegant structure really characterizes

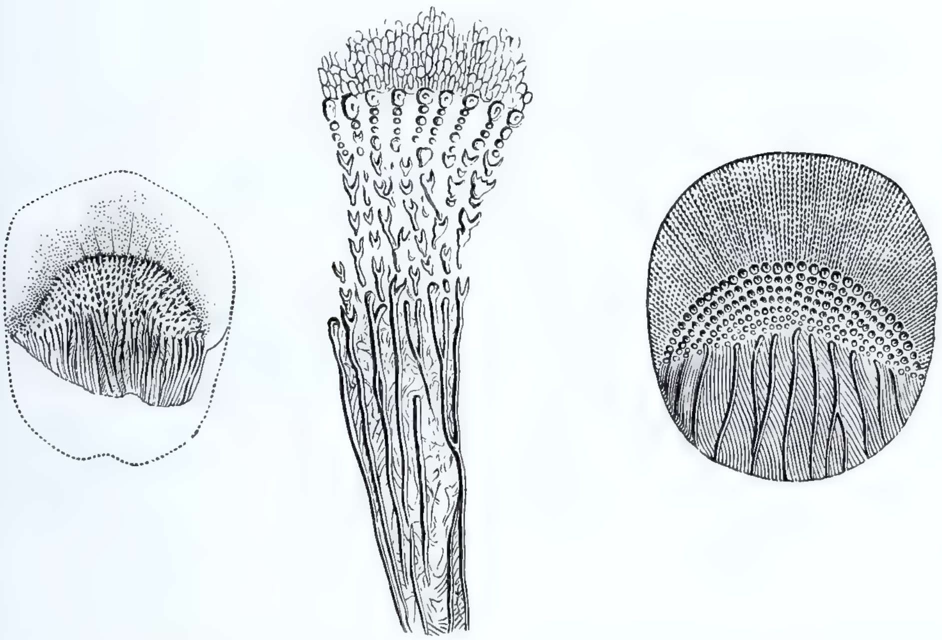

Fig. 6. The two left-hand figures represent the scale rom Wick of the natural size and its sculpture magnified ; the right-hand figure is copied from Pander's Monograph.

Glyptolepis is of great importance, for, in the first place, it enables one to discriminate between *Holoptychius* (whose scales have no semilunar area of backwardly directed points) and *Glyptolepis*, and in the second place, it places beyond a doubt the justice of Professor Pander's conclusion that the scale figured by Miller in the "Footprints," as appertaining to *Asterolepis*, really belongs to *Glyptolepis*.

Pander states that the rays of the median fins are supported upon long interspinous bones, and that the paired fins are very much approximated ; the very long pectorals extending far beyond the bases of the ventrals, which are very broad and strong.

Specimens which I have examined show, that the parietal bones of *Glyptolepis* are large, and, like the frontals, distinct from one

another; in their form and relative proportions, these bones very much resemble those of *Holoptychius*. There are three bones in the superior occipital region, one median and two lateral. A triangular, single or divided, squamosal fits in between the parietal, the external of the three superior occipital bones, and some indistinctly defined supratemporal and postorbital plates; again, as in *Holoptychius*. In the opercular apparatus, the operculum and suboperculum are large, subquadrate, and nearly equal in size. There are large dendrodont teeth (very well shown in a large specimen in Sir P. Egerton's collection) upon the inner side of the mandible. The principal jugular plates are large, but no specimen I have seen gives clear evidence of others. There is a well marked lateral line.

Apart from what has been done by Agassiz, Miller, and Pander,

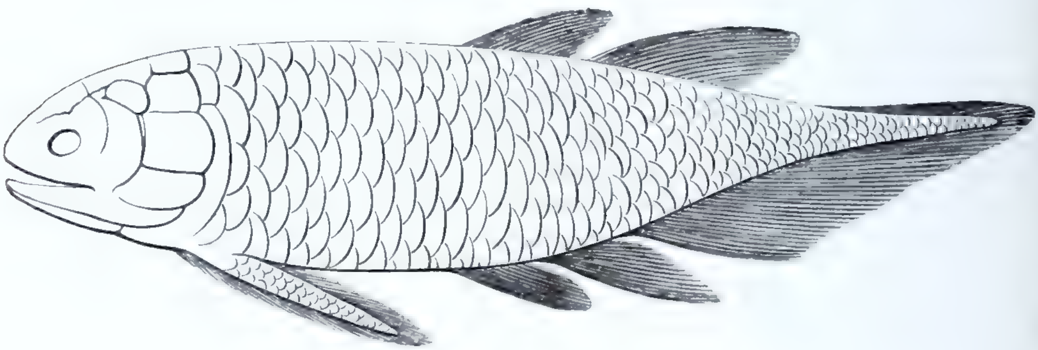

Fig. 7. Restoration of *Glyptolepis*.

I think I can venture to assert from my own investigations that the woodcut fig. 7 gives an essentially faithful restoration of *Glyptolepis*.[1] But a comparison of this figure with that of *Holoptychius*, given above, is sufficient to prove the close affinity of the two genera,—in fact, their family relationship.

Pausing now, to look back over the ground which has been traversed, we find that the six genera which have been discussed viz., *Glyptolæmus*, *Glyptopomus*, *Gyroptychius*, *Holoptychius*, *Platygnathus* and *Glyptolepis* possess the following characters in common:—Two dorsals, acutely lobate paired fins (ventrals of *Glyptolepis*); principal and lateral jugular plates, and no branchiostegal rays; more or fewer large teeth with grooved bases, and consequently folded dentine; sculptured scales and cranial bones,—among which last are to be noted three occipital plates,—large,

[1] It may be that the ventral fins are lobate, but I have seen no specimen justifying that conclusion.

distinct, parietals, and equally distinct frontals. In short, they constitute a family of Ganoids, which I propose to call GLYPTODIPTERINI, and which may again be subdivided into two groups, or subfamilies, the one, which might be called the rhombiferous Glyptodipterini, containing the genera *Glyptolæmus*, *Glyptopomus*, and *Gyroptychius*, with diphycercal tails, and for the most part rhomboidal scales ; and the other, which might be termed the cycliferous Glyptodipterini, containing *Holoptychius*, *Platygnathus*, and *Glyptolepis*, with heterocercal tails and cycloid scales.

Professor Pander has endeavoured to prove that the teeth known as *Dendrodus* belong to fishes of the genus *Gyroptychius*. The evidence brought forward in support of this view, however, appears to me to be hardly sufficient to demonstrate its accuracy ; though I think it extremely probable that the teeth and jaws, which have been referred to the genera *Dendrodus*, *Cricodus*, *Lamnodus*, *Platygnathus*, and *Rhizodus*, will turn out to belong to allies of *Gyroptychius*, or, in other words, to fishes belonging to the family of Glyptodipterini. And again I cannot adopt the family of "Dendrodonts" which Professor Pander has established for *Gyroptychius*, *Cricodus*, &c., partly because, as he defines it, it seems to me to separate naturally allied genera, and, still more, because the "dendrodont" character is quite as strongly marked in other fishes, *e. g.*, *Megalichthys*, which certainly do not belong to the same family as *Gyroptychius*, though undoubtedly related to it.

The resemblances which obtain between *Gyroptychius*, on the one hand, and *Osteolepis*, *Diplopterus*, &c., on the other, have been well pointed out by Professor Pander, whose Monograph upon the Saurodipterini is not less excellent than that already cited, though it should not be forgotten that Hugh Miller long ago published an excellent restoration of *Osteolepis*.[1] *Diplopterus* has, in fact, the elongated from, depressed head, forward orbits, long gape and conically tapering caudal end of the body, which characterize *Glyptolæmus*. The pectoral fins are similarly, though not so acutely, lobate, and the lobate ventrals are situated far back, as in the

[1] *See* "The Old Red Sandstone," Pl. iv. fig. 1, *Osteolepis major*. It appears from this figure that even the lobation of the pectoral fin had not escaped Hugh Miller, though he does not particularly refer to it in the text. Before Professor Pander's work appeared in this country, I had obtained from Caithness, by the well directed activity of Mr. Peach and placed in the Museum of Practical Geology, a series of specimens illustrating all the chief structural characters of *Osteolepis* as detailed above. The lobate pectorals of *Osteolepis* and *Diplopterus* are exhibited very well by specimens in the Hunterian and British Museum ; the fact that "small ganoid scales are continued upon" the bases of the pectorals being noted in the description of No. 567 in the Catalogue of the former Museum.

last-named genus. The second dorsal is over the anal, and the caudal fin is rhomboidal and diphycercal.

On the other hand, *Osteolepis*, though similar to *Diplopterus* in many essential respects, has a very inæquilobed tail, much like that of *Glyptolepis*. But in *Osteolepis*, as in its most nearly allied genera, the cranial bones and the scales are quite smooth. The three occipital plates of the skull remain distinct, but the other bones of the roof of the cranium have coalesced, so as to form two bucklers, an anterior and a posterior; in which, however, the outlines of the primitive cranial bones, which have, on the whole, an arrangement similar to that which obtains in *Glyptolæmus*, are traceable. There

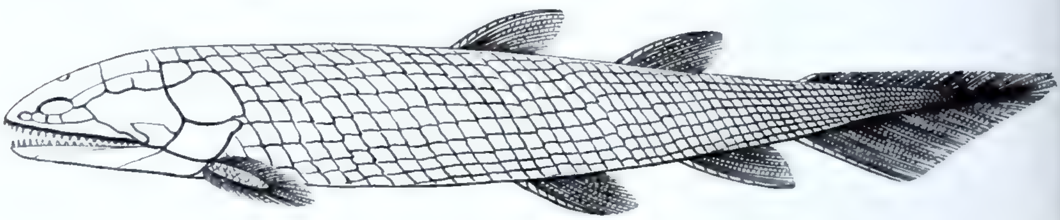

Fig. 8. Restoration of *Osteolepis* (after Pander).

are no lateral jugular plates, but the principal jugular plates are separated, anteriorly, by an azygos rhomboidal plate.

The family of the SAURODIPTERINI, characterized by its two dorsals; less acutely lobate paired fins; jugular plates and no branchiostegal rays; smooth scales and cranial bones (among which last are three distinct occipital plates, while the other cranial bones have more or less coalesced), is thus very distinct from, though allied to, that of the Glyptodipterini. It comprises not only the genera *Osteolepis*, *Diplopterus*, and *Triplopterus* (?), but also, as I believe, a genus which has a later range in time than these, viz., the *Megalichthys* of the Coal, although the want of acquaintance with the fins of this genus renders my conclusions as to its affinities less secure than I could wish.[1] Agassiz does indeed affirm that *Megalichthys* has lobate fins, in a passage cited above (p. 427); but as he merely mentions the fact incidentally, I do not like to lay too much

[1] Sir Philip Egerton long since arrived at and published this conclusion in his arrangement of the Fossil Fishes in Morris's Catalogue. More recently Prof. Pander expresses the same conviction in the following terms: "Sehr gerne möchten wir aber ein anderes Genus noch "zu den Saurodipteridæ bringen, das durch den Bau Seiner Kopfknochen; durch die Gestalt "seiner Schuppen, seiner Zähne und hauptsächlich durch die mikrospische Structur seiner "harten Theile sich eng an *Osteoleopis* anschliesst und aus der Kohlenformation herstammt. "Es ist der Genus *Megalichthys*, von dem wir leider die Beschaffenheit und Lage seiner "Flossen gar nicht kennen."—Pander, l. c., p. 5.

stress upon it. Nevertheless, the skull and scales of *Megalichthys* accord so closely, both histologically and morphologically, with those of the better known Saurodipterines, that I entertain little doubt as to its real place in the latter family.

Megalichthys has two principal, many lateral, jugular plates; and a single rhomboidal, azygos plate is placed between the anterior ends of the two principal jugulars. Between the upper margins of the opercula and in the upper occipital region, lie three bony plates, whose signification Professor Agassiz considers to be "somewhat enigmatical," but which really correspond exactly with the three bones which occupy the same position in the Glyptodipterini and Saurodipterini. What Agassiz terms the frontals are certainly the long parietals, whereas those which he calls "ethmoids" are the frontals. His "moignon intermaxil-"laire" is a crescentic shield, which terminates the head anteriorly, and presents distinct indications of a division into a number of pieces; the contour of the proper premaxillary portions, separated by a median suture, which form the lower and anterior boundary of the shield, being very well defined. The other parts entering into this shield represent, I believe, the prefrontals and the ethmoid. If it were amalgamated with the frontals and these with one another, we should have an almost exact reproduction of the anterior cranial buckler of *Osteolepis*. In a well preserved specimen of the skull of *Megalichthys* before me, the orbits are small circular cavities, placed at about the junction of the anterior and middle thirds of the head. They are bounded, in front and below, by a small triangular bone (like a lachrymal) as in *Polypterus*; below, by a small part of a large suborbital bone, whose anterior margin joins the premaxilla and its inferior margin the maxilla; below and behind, by another suborbital bone, fitted in between the preceding, the maxilla, and a postorbital bone. The maxilla, large and long, is narrow anteriorly, where it abuts upon the bone termed "preoperculum" by Agassiz; like the premaxilla, its edges are beset with small teeth. Agassiz says, "Le coté antérieur du mufle est "élégamment échancré au milieu et renflé en un bec, tres obtus, "qui porte dans notre exemplaire une grosse dent canine," and on making a transverse section of a *Megalichthys* snout I found a median, stout, backwardly projecting ridge of bone, containing two large alveoli, one on each side of the middle line. The one of these alveoli exhibits the section of the base of a large tooth with greatly folded dentine.

While the exoskeleton of *Megalichthys* is exceedingly similar to

that of *Diplopterus* and *Osteolepis*, the endoskeleton presents a remarkable advance on that of any other Saurodipterine, in that both the centra and the neural arches of the vertebral column are thoroughly ossified. Excellent specimens of these vertebræ are to be seen in the British Museum.

The Saurodipterini and Glyptodipterini being thus separated from other Palæozoic fishes, as well-defined families, perfectly distinct from one another, though closely allied by the community of characters displayed in the number, structure and disposition, of their fins, the absence of branchiostegal rays and their replacement by jugular plates; we have next to consider what other families of fish, if any, should be ranged alongside of them, or in other words, what are the limits and what the importance of the larger group, formed by the association of these families.

In the first place, I conceive there can be no doubt that the CTENODODIPTERINI, a family justly established by Professor Pander[1]

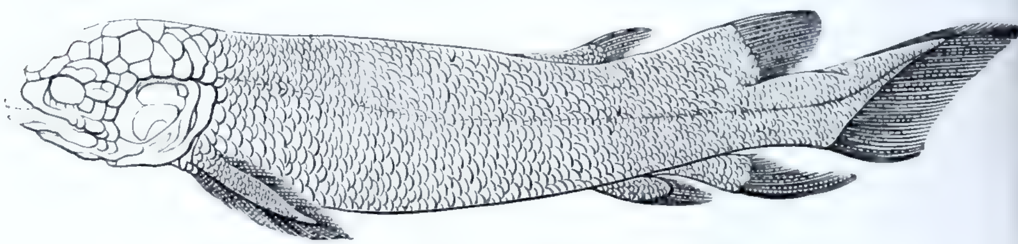

Fig. 9. Restoration of *Dipterus* (after Pander).

for the reception of *Dipterus* and its immediate allies, must take its place in close juxtaposition with the Saurodipterini and Glyptodipterini, seeing that it possesses all those structural peculiarities which are common to these two families. In fact, as Hugh Miller[2] originally pointed out in successive notices, *Dipterus* has the dorsal fins placed far back; acutely lobate pectorals and ventrals;[3] no branchiostegal rays, but jugular plates instead of them; and a single anal. The caudal extremity of the body tapers off to a point, and has the lower lobe of the fin very much larger than the

[1] Under the name of *Ctenodipterini*. Sir Philip Egerton has, I think, given good reasons for the slight change I have adopted. *Vide Mem. Geol. Survey*, 1861, p. 55.

[2] *See* "Old Red Sandstone," "Footprints of the Creator," and "Sketch Book of Popular Geology." It is much to be regretted that Professor Pander should have been wholly unacquainted with these works when he wrote his Monograph on the *Ctenododipterini*, and that he has consequently inadvertently failed to do justice to the great merits of Hugh Miller, who made known almost the whole organization of *Dipterus*, and anticipated the most important part of Prof. Pander's labours in this field.

[3] *See* Prof. Pander, l. c.

upper; the scales are cycloid. Thus far, in fact, the definition of Ctenododipterini agrees with that of the Glyptodipterini; but the former differ from the latter in the smoothness of their scales; in the structure of the roof of the cranium, whose constituent bones are anchylosed into a singular shield, presenting some resemblance to the cephalic shield of *Accipenser*; and lastly, and chiefly, in the peculiar form of the lower jaw, which much resembles that of a Cœlacanth, and in their dentition, so well made known by Hugh Miller, whose researches have been fully confirmed by Professor Pander.

In the next place, the true CŒLACANTHINI have a no less well-defined right to occupy a similar position.[1] I say the *true* Cœlacanthini, because the term "Cœlacanth" has been used by different

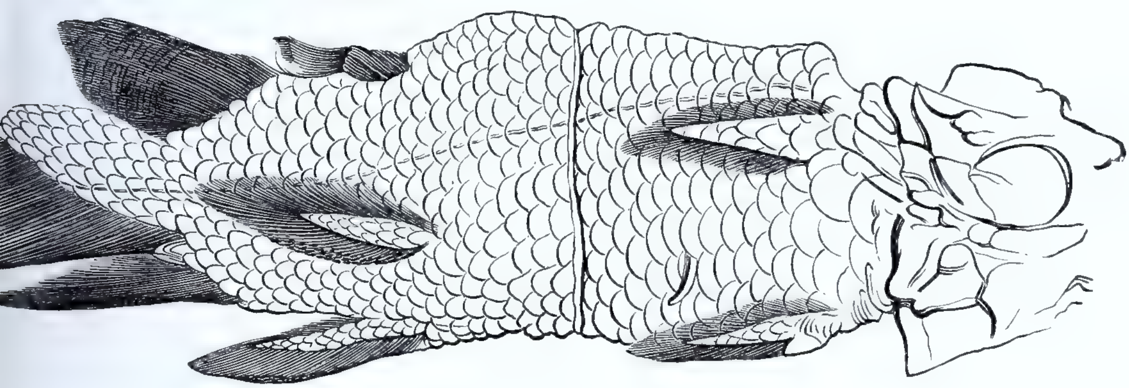

Fig. 10.[2] *Dipterus.*

palæontologists with such very different meanings, has been made in some cases to include so much, and in others to include so little, that I feel it to be necessary to define precisely the sense in which I employ it here. I intend it, then, to designate that family of fishes of which the genus *Cœlacanthus* of Agassiz is the type, a family which, thus restricted, is as well defined and natural a group as any in the animal kingdom, but, at present, can embrace only the genera *Cœlacanthus*, *Undina*, and *Macropoma*.

[1] Several years ago Sir Philip Egerton strongly drew my attention to the close affinity between the *Cœlacanthini* (*mihi*) and what I have termed the *Glyptodipterini*, particularly showing the importance of the lobate paired fins and of the double dorsals common to the genera of both families (which Sir Philip Egerton was inclined to group under the one head of '*Cœlacanths*'), and illustrating his views by a synopsis of the genera. From the study of that synopsis I trace the gradual clearing up of my own ideas respecting the difficult subject with which this preliminary essay attempts to deal.

[2] The woodcut, fig. 10, represents the same specimen as that figured by Sir Philip Egerton in "Siluria," ed. 2, p. 287, but of the natural size. It exhibits the characters of the paired fins of *Dipterus* remarkably well.

In order to make this clear, however, I must enter at some length into a historical and anatomical criticism of the Cœlacanths as a family of fishes.

In establishing this family (" Recherches," vol. ii. p. 168), Professor Agassiz dwells particularly upon the hollow fin rays of the typical genus; the absence of joints in some part of the length of most of those fin rays; the presence of interspinous bones in the caudal fin; the continuation of the vertebral column between the two lobes of that fin, and the prolongation of the caudal extremity beyond it as a filamentary appendage. With *Cœlacanthus*, *Undina*, *Macropoma*, *Hoplopygus*, *Uronemus*, *Holoptychius*, *Glyptosteus*, *Glyptolepis*, *Psammolepis*, *Phyllolepis*, *Ctenolepis*, and *Gyrosteus*, are associated; and it is a curious circumstance that while *Holoptychius* takes its place among the Cœlacanths, without any special demonstration of its right to that position, Professor Agassiz hesitates touching *Macropoma*, and, while admitting it into the family on account of the striking analogy of its general physiognomy, and of the form, arrangement, and structure of its fins, adds: " I must admit that side by side with these " resemblances, the two types exhibit profound differences," . . . . " which will perhaps, in the long run, necessitate another arrangement."

The idea that *Cœlacanthus* inclined more to *Holoptychius* than to *Macropoma*, appears to have found still more favour with Professor Agassiz at the time of the publication of his great work on the Fishes of the Old Red Sandstone; and the consequences of this inclination were the more important from the fact, that Agassiz held that the teeth, properly distinguished by Professor Owen under the name of *Rhizodus*, belonged to *Holoptychius*. For *Glyptolepis* and *Platygnathus* were undoubtedly closely allied to *Holoptychius*, while *Dendrodus*, *Lamnodus*, and *Cricodus* had much in common with *Rhizodus*; hence, as these dendrodont teeth were conceived by Agassiz to belong to the fish whose bony plates and scales had received the names of *Asterolepis*, *Bothriolepis*, &c., it was natural that he should include all these genera under the common title of " Cœlacanths;" while *Macropoma* and *Undina* were regarded with doubt, and, in fact, almost excluded from the group (" Vieux Grès Rouge," p. 64).

Here, however, I cannot but believe, that the founder of fossil ichthyology has, for once, gone off upon a wrong scent. For later investigations have made it, to say the least, extremely improbable that *Asterolepis* (Ag. & Miller) has anything to do with *Cricodus* or with *Holoptychius*, whatever may be the relation of the two latter genera; and I shall now endeavour to prove that, while

Cœlacanthus is so intimately connected with *Undina* and *Macropoma*, as to render the generic distinction of the three forms a matter of minute detail, its relations with *Holoptychius*, although clear and distinct so far as they go, are, at most, those of a member of the same suborder.

But first, what are the characters of the genus *Cœlacanthus?* This question is by no means so easily to be answered as might be imagined, but the following facts appear to furnish a conclusive reply to it.

The type species of *Cœlacanthus*, that on which the genus was founded by Agassiz, is the *C. granulatus* of the Magnesian Limestone; two figures of which are to be found in the "Recherches," while a third, representing another specimen, is given by Sir Philip Egerton in King's "Permian Fossils." Singularly enough, neither of these specimens retains its head, nor are the paired fins preserved; but the characters of the spinal column, of the median fins, of the scales, and of the tail, are so exactly those exhibited by the *Undina* of Münster (of which sundry complete specimens exist), that the very close affinity of the two genera is beyond doubt. Agassiz, in fact, proposes to distinguish them only by their teeth; *Cœlacanthus* having, in his opinion, conical and recurved, while *Undina* has flat, pavement-like and tuberculated teeth. That Münster was correct in assigning such teeth to *Undina* I have satisfied myself by the examination of a well-preserved specimen of *U. Köhleri* in Lord Enniskillen's collection; but what evidence is there that *Cœlacanthus* has a different dentition? Agassiz was led to believe that the teeth of the latter genus are conical, by the fact that the specimen of a fish named by him *C. Münsteri* has such teeth. I am again indebted to the Earl of Enniskillen, of whose collection this specimen forms a part, for the opportunity of verifying the statement; but I must at the same time express my entire concurrence in the opinion previously expressed to me by Sir Philip Egerton, that the so-called "*Cœlacanthus*" *Münsteri* is not a *Cœlacanthus* at all.

For, as I have stated above, there can be no doubt that *Cœlacanthus* (*C. granulatus* being the typical species) was, in all the great features of its organization, similar to *Undina*; so that, contrariwise, any fish which differs in essentials very widely from *Undina* can be no *Cœlacanthus*.

But *Undina* has two dorsal fins, each supported by but a single very peculiarly shaped, interspinous bone; it has a large caudal fin, whose rays are supported by interspinous bones, and which is divided

into two equal lobes by the unossified spinal column; the latter extending beyond the caudal fin as a tufted appendage, or second caudal, provided with very short fin rays. There is a single anal fin; the pectoral and ventral fins are well developed and obtusely lobate; the pelvic bones are remarkably large, and are united together by transverse branches, which extend from the posterior extremities of each and meet in the middle line; there are no dorsal ribs and no proper branchiostegal rays, but instead of them, two broad principal jugular plates. Finally, the scales, large, thin, and cycloid, are ornamented with elongated splashes and dots of enamel. On the other hand, "*Cœlacanthus*" *Münsteri* exhibits no

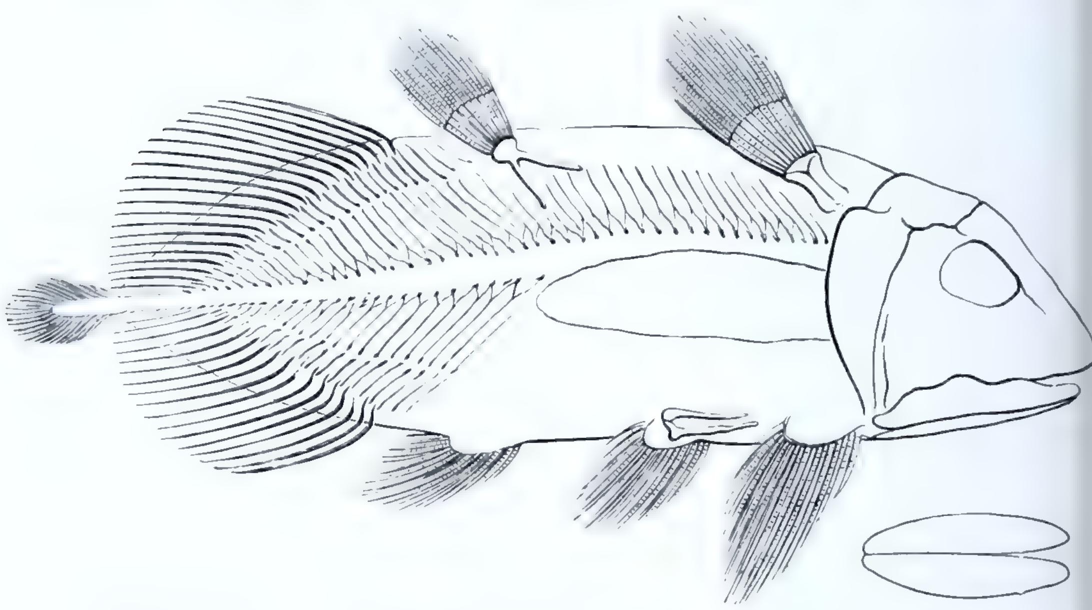

Fig. 11. Restoration of *Undina*. (Partly after Münster, partly from Lord Enniskillen's specimen. Below the head are the contours of the jugular plates.)

one of the positive characters here enumerated, while it *has* ribs attached throughout the dorsal region; in fact, I am inclined to consider it the type of a new genus allied to *Phaneropleuron*.

I have seen no specimens of the other species of *Cœlacanthus* enumerated by Agassiz, and I can therefore say nothing about them. But *Cœlacanthus caudalis* (Egerton) is a true Cœlacanth, as I have convinced myself by examination of the specimen, to which the figure in King's "Permian Fossils" does not quite do justice.

As the case stands, then, it appears that there is no evidence that the supposed distinction between *Cœlacanthus* and *Undina* really obtains; while, on the other hand, a recent careful comparison of

well-preserved specimens of *Undina* and of *Macropoma* has convinced me that these two genera are not much less closely allied.

All the structural characters, in fact, which have been enumerated above among the peculiarities of *Undina* are equally well marked in *Macropoma*, except that, hitherto, I have been unable to meet with the caudal appendage in the latter, and that the teeth are more distinct and cylindrical. But further than this, as Dr. Mantell originally suspected, and as Professor Williamson has since demonstrated, *Macropoma* exhibits the peculiarity, without a parallel so far as I know, among fishes of other families, of having the walls of its air bladder ossified. Now, I find good evidence of the existence of a similarly ossified air bladder, not only in *Undina*,

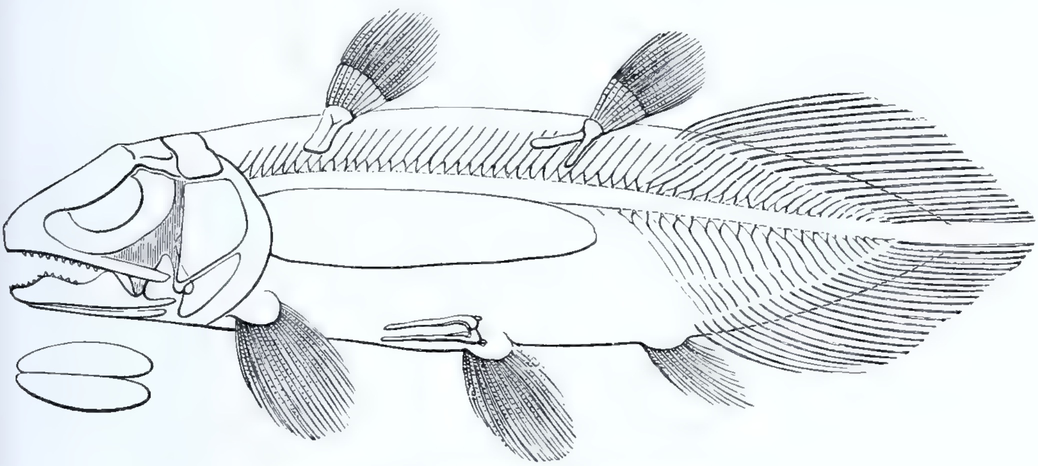

Fig. 12. Restoration of *Macropoma*.

but in a well-preserved specimen of a new genus of Cœlacanth, from the Lias (described in the subjoined note by Sir Philip Egerton), in the Museum of Practical Geology.[1]

[1] *Holophagus Gulo.*

Mr. Harrison's specimen wants the anterior portion from the dorsal and pectoral fins forwards. From the insertion of the dorsal fin to the extremity of the tail it measures $11\frac{1}{2}$ inches, and $4\frac{1}{2}$ inches in depth. The stomach is distended with a recently swallowed *Dapedius*, and a large coprolite occupies the rectum. The first dorsal fin springs (as in *Macropoma*) from a single disc, resulting from the coalescence of the interneural spines. It contains eight long, thick, undivided, and multiarticulate rays. They are beset with numerous short spines or tubercles. The second dorsal is situated 4 inches behind the first. Between the two is seen a strong bifurcate interneural ossicle, which has been displaced forwards from its proper position at the base of the fin. The second dorsal fin contains sixteen rays. The anterior ones are short and slender. The succeeding ones are long, broad, and multiarticulate but not tuberculate. The base of the fin is obtusely lobate, with a scaly investment. The pectoral fins are much mutilated. Judging from what remains of them, and from some indistinct impressions, they seem to have been of great size. The anal fin occurs immediately

Thus, leaving open the question as to the identity of *Cœlacanthus* with *Undina*, and also that whether *Uronemus* and *Hoplopygus* (which I have not seen, and concerning which no details are given by Agassiz) are Cœlacanths, or not; it appears to be certain that fishes closely allied to *Cœlacanthus granulatus*, and known under the generic appellations of *Undina* and *Macropoma*, form an exceedingly well-defined family, to which the term CŒLACANTHINI may with propriety be restricted, and which has ranged in time, with remarkably little change, from at least as early as the Permian formation to the Chalk, inclusive.

The Cœlacanthini, as thus understood, are no less distinctly separated from other fishes than they are closely united to one another. In the form and arrangement of their fins; the structure of the tail and that of the cranium; the form and number of the jugular plates; the dentition; the dorsal interspinous bones; the pelvic bones; the ossified air bladder; the Cœlacanthini differ widely from either the Saurodipterini, the Glyptodipterini, or the Ctenododipterini; but, on the other hand, they agree with these families and differ from almost all other fishes, in the same respects as those in which the several families just mentioned, have been shown to agree with one another; viz., the number of the dorsal fins, the lobation of the paired fins, the absence of branchiostegal rays, and their replacement by jugular bones.

Their special affinities among these three families appear to me to lie chiefly with the Ctenododipterini: the scales, the arrangement

below the second dorsal fin, with which it corresponds in form and structure, but contains many more rays. The ventral fins are mutilated, but their position below the first dorsal fin is indicated by the preservation of a pair of strong T-shaped pelvic bones, having their longer limbs directed forwards, and nearly reaching the base of the pectoral fins. The caudal fin is of great size, and presents in an eminent degree the most special and characteristic feature of the *Cœlacanthus* family, namely, the interposition, in the caudal region, of an interneural between the neural and dermo-neural spines. The base of this spine abuts upon the extremity of the neural spine, and unites with the true fin-ray by an overlap or splice. This structure coincides with that observed in *Undina*. In *Macropoma* the bone of the interneural spine is bifurcate for the reception of the distal extremity of the neurapophysis. A small supplemental fin extends an inch beyond the larger caudal fin, as in *Undina* and *Cœlacanthus*. The notochord is unossified. The apophyses, both above and below, have very wide bases. The scales are curvilinear, and covered with a vermiculate pattern on the upper surface, occasionally broken up into small tubercles.

In the Woodwardian Museum at Cambridge there is the head and part of the trunk of a *Cœlacanthus*, from the Kimmeridge Clay at Cottenham. The head shows the frontals, prefrontals, and lower jaw, with the tympanic attachments. The glossohyal plate is double, as in *Holoptychius*. The scales are roughly undulate, coarser in pattern than in *Undina*, *Cœlacanthus*, and *Holophagus*, but not absolutely tuberculate, as in *Macropoma*. One fin is preserved, probably the left pectoral. It is lobate, broad and strong. The operculum is triangular, the frontals short, and the prefrontals descend at an abrupt inclination.

of the teeth, and the form of the lower jaw in the two families presenting many curious analogies.

The Glyptodipterine family contains, as we have seen, both cycliferous and rhombiferous genera. Following out the alliances of the former subfamily, we have found reason to include the cycliferous Ctenododipterini and the cycliferous Cœlacanthini in the same larger, or subordinal, group with the Glyptodipterini. If, on the other hand, we now trace out the congeners of the rhombiferous subfamilies, we arrive, as has been seen, at the Saurodipterini, and the question now remains, What other rhombiferous Ganoids naturally arrange themselves at this end of the series?

So far as I am aware, there is no other fossil rhombiferous Ganoid which comes within the scope of the sum of characters common ot

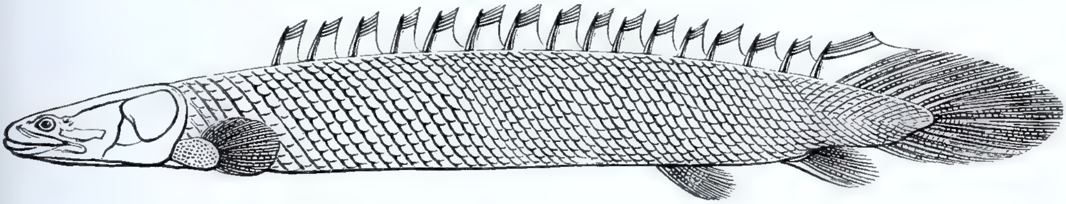

Fig. 15. Figure of *Polypterus* (after Agassiz).

the Saurodipterini, Glyptodipterini, Ctenododipterini, and Cœlacanthini; but among recent fishes there is one, Polypterus, which very nearly approaches the required standard, and is unquestionably closely allied to the Saurodipterini.

Polypterus, in fact, has an elongated body, with a depressed head, and a conically tapering caudal extremity. The orbits are situated in the fore part of the head, while the gape extends far back. There are two large principal jugular plates, without lateral or median plates. The pectoral arch is covered inferiorly by two triangular osseous plates, which meet in the middle line, and are superficial to the so-called coracoids. The pectoral and ventral fins are lobate. The caudal fin is rhomboidal and nearly diphycercal.[1]

A comparison of these characters with those which have been assigned to *Glyptolæmus*, or to *Osteolepis*, reveals at once the close connexion of the three genera,[2] from which however *Polypterus* differs in many important particulars.

[1] *See* the careful account of the tail of *Polypterus*, by Kölliker, "Ueber das Ende der Wirbelsäule der Ganoiden."

[2] I do not know that any one has hitherto pointed out in detail the very close relation between *Polypterus* and the fossil genera enumerated above; but Professor Pander has

Thus the parietal bones of *Polypterus* are much smaller, in proportion to the frontals, than are those of either *Osteolepis* or *Glyptolæmus*, and with age they unite with one another and with the frontals, into a continuous shield, as seems to have been the case in *Dipterus*.

The upper part of the occipital region is covered by a number of more or less irregular plates, which, however, may be readily shown to correspond with dismemberments of the three plates found in the Saurodipterini, &c. There are neither lateral, nor median, jugulars, the teeth have simple pulp cavities; and what is most remarkable, the dorsal fin, instead of being double, is incompletely broken up into a number of pinnules, which extend for nearly the whole length of the back. Furthermore, *Polypterus* has a spiracle, a structure of which I find no trace in any of the fossil genera.

It may conduce to clearness if, before proceeding farther, I now endeavour to put the results of the preceding statements into a readily comprehensible and definite form, and show their bearing upon the classification of the Ganoids, and more particularly upon that of the fossil Ganoidei. To this end I have prepared the following synoptical table:—

ORDO GANOIDEI.

SUBORDO I.—AMIADÆ.

SUBORDO II.—LEPIDOSTEIDÆ.

SUBORDO III.—CROSSOPTERYGIDÆ.

Fam. I.—POLYPTERINI.

Dorsal fin very long, multifid; scales rhomboidal.

Polypterus.

Fam. 2.—SAURODIPTERINI.

Dorsal fins two; scales rhomboidal, smooth; fins subacutely lobate.

Diplopterus, *Osteolepis*, *Megalichthys*.

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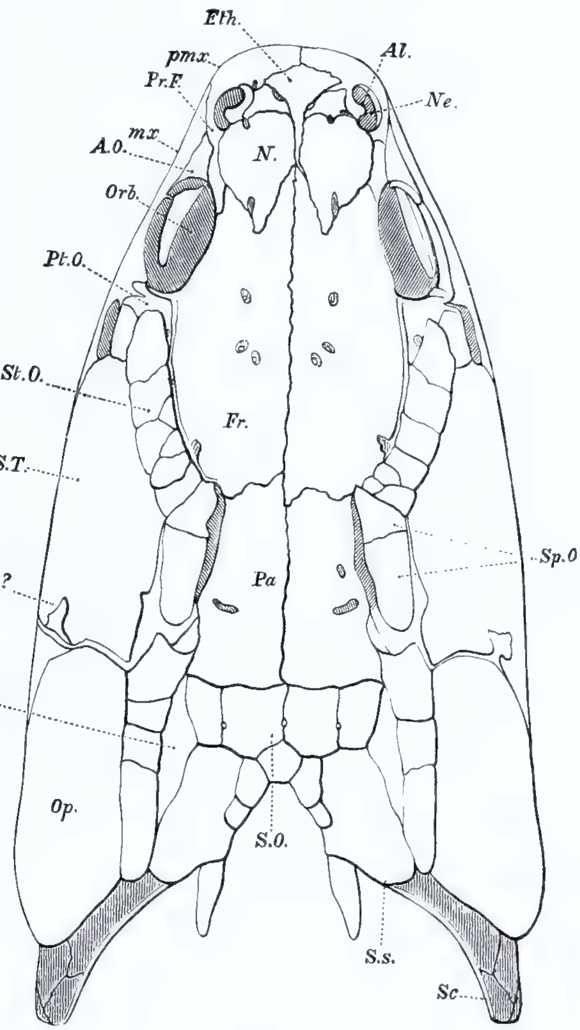
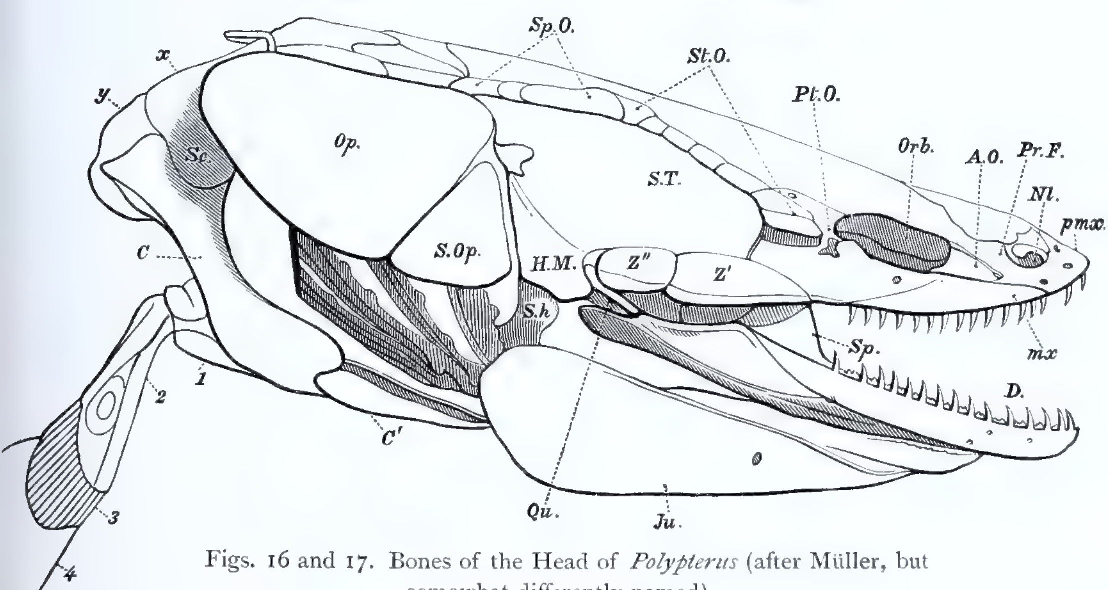
enunciated conclusions nearly similar to my own in the following passage (Ctenodipterinen, p. 3): —

"Ueberhaupt ist es merkwurdig zu sehen wie *Polypterus* so ganz in den Hintergrund "gestellt wird, Herr J. Müller (Ueber d. Bau.) sagt ausdrücklich 'Fur den *Polypterus* kenne "'ich unter allen fossilen Ganoiden keine analogie.' Und Herr Pictet wiederholt dasselbe "gleichfalls, 'aucun fossile n'a été rapproché de ce genre remarquable.' Wir werden in "Zukunft sehen dass wenn man überhaupt ein Recht hat, wie es doch wahrscheinlich ist, die "ausgestorbenen Geschlechter der Devonischen Formation jetzt noch lebenden Fischen an "die Seite zu stellen, mehrere durch ihre Zahnbau, durch die grossen Knochen-platten und "die Stelle der Kiemenhaut-strahlen, durch den Bau der Kopfknochen, u.s.w., eine "grössere analogie mit dem *Polypterus* als seinen Amerikanischen Zeitgenossen besitzen."

In his subsequent memoirs Prof. Pander has not followed out to their logical result the views so sagaciously indicated in this paragraph, which I think would be identical with those I had arrived at before I read it, and now publish.





Figs. 16 and 17. Bones of the Head of *Polypterus* (after Müller, but somewhat differently named).

SUBORDO III.—CROSSOPTERYGIDÆ—*Continued.*

Fam. 3.—GLYPTODIPTERINI.

Dorsal fins two; scales rhomboidal or cycloidal, sculptured; pectoral fins acutely lobate; dentition dendrodont.

Sub-fam. A. with rhomboidal scales.

Glyptolæmus, *Glyptopomus*, *Gyroptychius.*

Sub-fam. B. with cycloidal scales.

Holoptychius, *Glyptolepis*, *Platygnathus* [*Rhizodus*, *Dendrodus*, *Cricodus*, *Lamnodus*].

Fam. 4.—CTENODODIPTERINI.

Dorsal fins two; scales cycloidal; pectorals and ventrals acutely lobate; dentition ctenodont.

Dipterus, [*Ceratodus? Tristichopterus?*].

Fam. 5.—PHANEROPLEURINI.

Dorsal fin single, very long, not subdivided, supported by many interspinous bones; scales thin, cycloidal; teeth conical; ventral fins very long, acutely lobate.

Phaneropleuron.

Fam. 6.—CŒLACANTHINI.

Dorsal fins two, each supported by a single interspinous bone; scales cycloidal; paired fins obtusely lobate; air bladder ossified.

Cœlacanthus, *Undina*, *Macrcpoma.*

SUBORDO IV.—CHONDROSTEIDÆ.

SUBORDO V.—ACANTHODIDÆ.

Considering the Ganoidei, as defined by Müller, to form an order of the class *Pisces*, and adopting the four groups typified by *Amia Lepidosteus*, *Accipenser* and *Acanthodes*, respectively, as sub-orders, without thereby prejudicing the question as to whether other suborders may not be required, I propose to establish another and equivalent group, or suborder, to comprise the existing *Polypterus* and all those extinct Ganoids which, like it, fall within the range of the following definition:—

Dorsal fins two, or, if single, multifid or very long; the pectoral and usually the ventral fins, lobate; no branchiostegal rays, but two principal, with sometimes lateral and median, jugular plates, situated between the rami of the mandible; caudal fin diphycercal, or hetero-cercal; scales cycloid or rhomboid, smooth or sculptured.

On the suborder thus defined I propose to confer the title of CROSSOPTERYGIDÆ,[1] in consideration of the peculiar manner in which the fin rays of the paired fins are arranged, so as to form a fringe round a central lobe, which constitute so marked a character of all the genera belonging to the group at present known.

[1] κροσσωτὸς, πτέρυξ, "fringed fin." "Crossotopterygidæ" would perhaps be more correct, but the shorter compound is preferable.

The characters of five of the six families which compose this suborder have been given, incidentally, in the preceding pages, but the table contains another family whose collocation with the rest requires justification.

This is the family of the PHANEROPLEURINI, which I have established to contain the singular genus *Phaneropleuron*, described at length in this Decade (p. 505) and figured in Plate III. The general character of this fish, its thin cycloid scales, the mode of termination of its caudal extremity, and its remarkable, very acutely lobate, ventral fins, lead me to entertain very little doubt that its right place is among the Crossopterygidæ, and in the neighbourhood of the Glyptodipterini and Cœlacanthini, though I have not yet been able to obtain a very good view of its jugular plates. But the very long, single, dorsal fin, the great length and acute lobation of the ventral fins, which seem to have been longer than the pectorals and the complete ossification of the costal elements and neural arches throughout the vertebral column, separate *Phaneropleuron* alike from the Glyptodipterini and the Cœlacanthini. From the Ctenododipterini it is separated not only by these characters, but by its dentition. Under these circumstances the only course seems to be to regard it as the type of a distinct family.

The group of Crossopterygidæ, as thus established, appears to me to have many remarkable and interesting zoological and palæontological relations. Of the six families which compose it, four are not only Palæozoic, but are, some exclusively and all chiefly, confined to rocks of Devonian age,—an epoch in which, so far as our present knowledge goes, no fish belonging to the suborders of the Amiadæ or Lepidosteidæ (unless *Cheirolepis* be one of the latter) makes its appearance. Rapidly diminishing in number, the Crossopterygidæ seem to have had several representatives during the Carboniferous epoch, but after this period (unless *Ceratodus* be a Ctenododipterine) they are continued through the Mesozoic age only by a thin, though continuous, line of Cœlacanthini, and terminate, at the present day, in the two or three known species of the single genus *Polypterus*. *Polypterus*, however, is clearly related to the rhombiferous Crossopterygians, or in other words, to exactly that group of whose existence we have no knowledge in any Mesozoic, or Tertiary, formation; while the Ctenododipterini and Cœlacanthini, which depart most widely from *Polypterus*, are those which continue the line of the Crossopterygidæ from the Palæozoic to the end of the Mesozoic epoch. Thus both ends of the Crossopterygian series appear, if I may use the expression, to be cut off from the

modern representatives of the suborder; *Polypterus* being separated from those members of its suborder with which it has the closest zoological relations, by a prodigious gulf of time, and from the fossil allies which are nearest to it in time, by deficient zoological affinity. I may make my meaning more intelligible by a diagram, however.

PALÆOZOIC.

Ctenododipterini, Phaneropleurini, Glyptodipterini, Saurodipterini, Cœlacanthini.

MESOZOIC.

Cœlacanthini.

TERTIARY.

RECENT.

Polypterini.

Here it is obvious that, in time, the Polypterini are twice as remote from their immediate zoological affines, the Saurodipterini and Glyptodipterini, as they are from their more distant connexions, the Cœlacanthini.

It seems singular that while the line of the rhombiferous Crossopterygidæ has so distinct a modern representative, the cycliferous

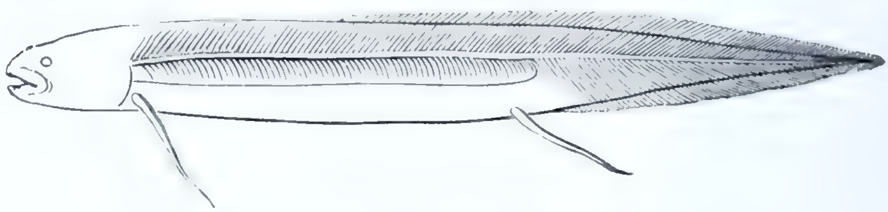


Fig. 18. Diagram of *Lepidosiren.*

Crossopterygidæ seem to have died and left no issue at the end of the Tertiary epoch. But without wishing to lay too much stress upon the fact, I may draw attention to the many and singular relations which obtain between that wonderful and apparently isolated fish, *Lepidosiren*, sole member of its order, and the cycloid Glyptodipterine, Ctenododipterine, Phaneropleurine, and Cœlacanth Crossopterygidæ. *Lepidosiren* is, in fact, the only existing fish whose pectoral and ventral members have a structure analogous to that of the acutely lobate, paired fins of *Holoptychius*, of *Dipterus* or of *Phaneropleuron*, though the fin rays and surface scales are still less developed in the modern than in the ancient fish. The endoskeleton of *Lepidosiren*, again, is, as nearly as possible, in the same condition as that of *Phaneropleuron*, and is more nearly similar to the skeleton of the Cœlacanths than that of any other recent fish; while, perhaps, it is not stretching the search

for analogies too far to discover in the stiff-walled lungs of *Lepidosiren*, a structure more nearly representing the ossified air bladder of the Cœlacanths than any with which we are at present acquainted, among recent or fossil fishes. Furthermore, *Lepidosiren* is the only fish whose teeth are comparable in form and arrangement to those of *Dipterus*.[1] Though *Lepidosiren* may not be included among the Crossopterygidæ, nor even in the order of the Ganoidei, the relations just pointed out are not the less distinct ; and, perhaps, they gain in interest when we reflect, that while *Polypterus*, the modern representative of the rhombiferous Crossopterygidæ, is that fish which has the most completely lung-like of all air bladders, *Lepidosiren*, which has been just shown to be, if not the modern representative of the cycliferous Crossopterygidæ, yet their "next of kin" is the only fish which is provided with true lungs. These are unquestionable facts. I leave their bearing upon the great problems of zoological theory to be developed by every one for himself.

The preceding discussion of the affinities of the Devonian genera, *Osteolepis*, *Diplopterus*, *Glyptolæmus*, *Glyptopomus*, *Gyroptychius*, *Holoptychius*, *Glyptolepis*, *Dendrodus*, *Phaneropleuron*, *Dipterus*, was an indispensable preliminary to the consideration of the main question with which I proposed to deal in the present essay, viz., What, and how many, groups of fishes are represented in the Fauna of the Devonian epoch? a Fauna which presents a surpassing interest, when we recollect that it comprises the oldest assemblage of vertebrate animals, of which we possess a more than fragmentary knowledge ; that its constituents abound in certain localities ; and that, for many years past, they have been the subject of careful and repeated collection and investigation. An examination of the data collected up to the present time has led me to the following conclusions, some of which are already current, while others are new :—

1. No vertebrate animal higher in the scale than fishes is as yet certainly known to have been found in any rock of Devonian age. In fact, until demonstrative stratigraphical evidence of the Devonian age of the well-known Elgin beds is obtained, the bearing of the palæontological evidence against that conclusion is too strong to allow of its being entertained.

2. Of the six orders of the class Pisces, three, namely, the DIPNOI, MARSIPOBRANCHII, and PHARYNGOBRANCHII, are certainly not represented by any known Devonian fish. In endeavouring to estimate the value of this negative fact, we must recollect that no fish belonging

[1] Prof. Pander has drawn attention to the resemblance of the teeth of his genus *Holodus* to those of *Lepidosiren*, but it is not clear that he regards *Holodus* as a Ctenododipterine.

to either of these orders is at present known in the fossil state; that they are represented by a very small number of genera and species in our existing Fauna; finally, that the Pharyngobranchii, from their very nature, could hardly be preserved in a recognizable state, even in such fine mud as that of the Oxford clay, or the Solenhofen slates, and that of the Marsipobranchii nothing but the horny teeth could be expected to escape destruction. *Lepidosiren*, on the other hand, might have left as definite traces of its existence as *Dipterus*, and hence its entire absence in the fossil state is a negative fact of greater value.

3. The ELASMOBRANCHII abounded, teeth and spines testifying to the numerous and diverse genera which haunted the Devonian seas. It is more difficult to say to what sections of the order these genera belonged, as the only Devonian Elasmobranch whose whole structure can be restored with any certainty is *Pleuracanthus*, a fish which belongs to a family distinct from any now living.

4. The GANOIDEI, as I have endeavoured to show above, are largely represented by a suborder, the Crossopterygidæ, which drops into comparative insignificance in later ages. Of the existence of Amiadæ there is no evidence, and even if we include *Tharsis*, *Thrissops*, and *Leptolepis* under this suborder, they are scanty in all later formations; but what is much more remarkable is the apparent, entire, or almost entire, absence of the Lepidosteidæ, a suborder which obtains such a prodigious development in the Mesozoic epoch. The nature of the Acanthodidæ, and the question whether there is any reason to suspect the existence of Chondrostei during the Devonian epoch will be considered by-and-bye.[1]

[1] The determination of the characters of the families of Lepidosteidæ and of the limits of the suborder is a difficult problem, of which I hope to treat more fully hereafter. One interesting fact results from my investigations, so far as they have hitherto gone, viz., that *Lepidosteus* belongs to a totally distinct family from its Mesozoic allies, whether "Sauroids" or "Lepidoids." The Pycnodonts and Hoplopleuridæ do not appear to me to belong to the Lepidosteidæ, and I doubt their being true Ganoids. For the present I propose the following as a sketch of an arrangement of the Lepidosteidæ.

LEPIDOSTEIDÆ.

Heterocercal Ganoids with rhomboidal scales; branchiostegal rays; non-lobate paired fins; a preoperculum and an interoperculum.

Fam. 1. Lepidosteini.

Maxilla divided into many pieces; branchiostegal rays few and not enamelled.

Lepidosteus.

Fam. 2. Lepidotini.

Maxilla in one piece; branchiostegal rays many and enamelled; the anterior ones taking the form of broad plates.

(a) *Œchmodus*, *Tetragonolepis*, *Dapedius*, *Lepidotus*, *&c.*

(b) *Eugnathus*, *Pachycormus*, *Oxygnathus*, *&c.*

(c) *Aspidorhynchus.*

Perhaps the genera marked a, b, c, should form distinct sub-families.

5. The TELEOSTEI have hitherto been supposed to be entirely absent from formations of Palæozoic age, and no doubt they do not exist under those forms which are most familiar to ichthyologists acquainted with marine fishes, or with the fresh-water fishes of temperate climates; but, nevertheless, I shall now endeavour to show that there are grounds for something more than a suspension of judgment, as to the validity of the ordinary doctrines held upon this subject.

The remarkable genera *Coccosteus* and *Pterichthys* are those which, among all Devonian fishes, have been by common consent regarded as the most heteroclite and anomalous, some writers having gone so far, in fact, as to imagine that these hard cased vertebrates offered us a transition to the shelled Invertebrata.

Nevertheless, I trust I shall be able to show that the one of these two closely allied genera—*Coccosteus*—is best, indeed, I may say only, to be understood, by comparing its bony shields with those which cover the roof of the cranium and the anterior part of the body of certain existing Siluroid Teleosteans.

To this end, however, I must first give the conception of the structure of *Coccosteus* which my own investigations, guided by those of my predecessors, Agassiz, Miller, Egerton, and Pander,[1] have led me to form.

The superior wall of the skull only, seems to have been ossified in this fish, and forms a great shield, which may be roughly said to have a hexagonal figure. The posterior and postero-lateral sides of the hexagon are pretty nearly straight lines, while the anterior side is rounded off, to form the snout, and the antero-lateral sides, the longest of all, have their anterior moieties deeply excavated, to constitute the upper part of the walls of the orbit. From before backwards, in the median line, the contour of the cranial shield is nearly straight, but from side to side it is convex, in consequence, more particularly, of the downward inflexion of its postero-lateral angles. The sutures, which separate the various constituent bones of the skull, may readily be confounded with certain superficial grooves of a totally different import, but, by grinding away the outermost layer of bone, this source of error is avoided; and it is then seen that the cranial sutures have the arrangement represented in the woodcut, fig. 19, and define the several bones from one another with great sharpness.

In the middle line, behind, they mark off a symmetrical, trape-

[1] Compare Agassiz, "Monog. des Poissons Fossiles du Vieux Grès Rouge;" H. Miller, "Old Red Sandstone" and Quart. Journ. Geol. Soc. 1859; Pander, "Ueber die Placodermen des Devonischen Systems, 1857;" Sir P. Egerton, "Remarks on the Nomenclature of the Devonian Fishes," Quart. Journ. Geol. Soc. 1859.

zoidal bone, S. O., which presents a short peg-like process in the middle of its posterior edge, and has a peculiar raised pattern upon its under surface. In front, this bone is articulated with the singular four-rayed bone Fr. The posterior ray (with which S. O. is connected) is the shortest and broadest of the four, while the lateral rays are the longest and the narrowest, the anterior ray holding a middle position in this respect. The edges of the anterior and of the lateral rays are variously indented, apparently to form an interlocking suture with the adjacent bones, while the posterior ray is deeply excavated to unite with S. O. A third bone, much smaller than the preceding, succeeds

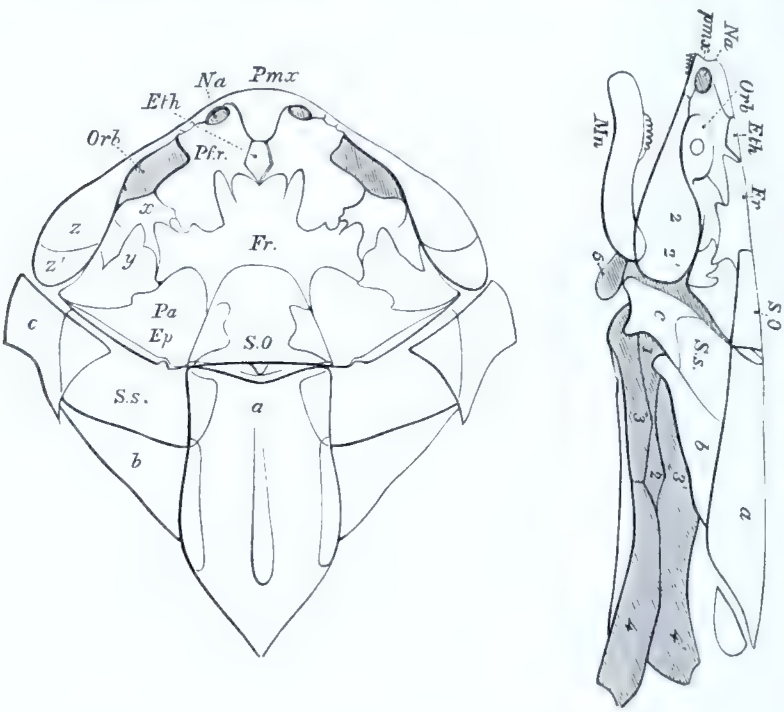


Fig. 19. Bones of the head and of the cuirass of *Coccosteus*.

them anteriorly, and appears to be separated by a transverse suture from a fourth median bone (Pmx.), whose rounded free edge forms the anterior contour of the snout. In well-preserved specimens, this edge is seen to be beset with small, projecting, spine-like tubercles or teeth. The lateral portions of the skull are constituted, proceeding as before, from behind forwards, as follows : a triangular bone (Pa. Ep.), one of whose sides, directed outwards and backwards, forms the postero-lateral side of the hexagon above referred to, unites, by its inner edge, with the bone S. O., and, by its anterior edge, partly with Fr. and partly with another bone (*y*). These edges are irregularly sinuous, and form a squamous suture with the neighbouring bones. The posterior edge

of Pa. Ep. presents, near its inner extremity, a sort of socket, with which a peg developed from the plate S. s. is articulated.

An irregularly triangular bone (y) is connected with the anterior edge of Pa. Ep., and forms the posterior angle and part of the antero-lateral edge of the skull. It is succeeded by another irregular bone (x), which enters into the posterior and upper wall of the orbit, and unites internally with Fr., and anteriorly with a larger and still more irregular bone Pfr. The latter is connected internally with Fr., Eth. and Pmx.; while externally it sends off, rather in front of the middle of its length, a short process, which passes directly downwards and divides the

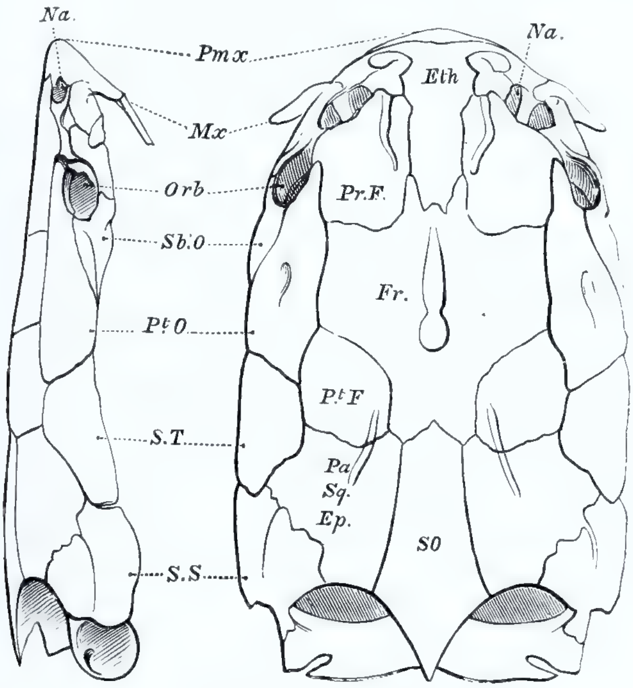


Fig. 20. Bones of the head of *Clarias*.

orbital cavity (Orb.) from the nasal cavity (Na.). Extending from the lower end of this process to the postero-lateral angle of the skull, bounding the orbit below, and fitting in by its convex margin, to a concave excavation of the bones x, y, is a large spatulate bony plate, narrow in front, broad and expanded behind, and composed of two pieces, z and z'.

The cranio-facial shield thus composed is succeeded by an osseous girdle, which defended the anterior part of the body like the back and breast plates of a mediæval warrior, and is divisible into two portions, the dorso-lateral and the ventral shields—the former composed of nine pieces, the latter of six. Of the nine pieces of the dorso-lateral shield,

seven are closely articulated together, while the other two, small and comparatively insignificant, (and not represented in the dorsal view, fig. 19) were placed loosely at the sides of the posterior end of the great median plate of the seven. This plate *a* corresponds in width, anteriorly, with the cranial bone S. O.; it widens a little behind the middle of its length, and then rapidly tapers to a point. From the middle of its under surface it sends down a strong bony crest, deeper behind than in front, while its lateral edges overlap and unite, by a squamous suture, with the plates S.s. and *b*.

S.s. is a four-sided plate, articulated with Pa. Ep. in the manner before mentioned, while behind it overlaps the triangular plate *b*, and below is overlapped by the plate *c*. The latter is so constantly thrown out of its place in specimens where the connexion between *a*, *b* and S.s is perfectly retained, that I suspect it rather overlapped than was suturally united with S.s.

The ventral shield appears to me to have had no direct connexion with the dorsal. I have examined a large number of specimens with reference to this point, but I have never discovered the least evidence of a sutural union between any two elements of the two shields, though the respective constituents of each shield are constantly met with in all stages of union and disunion. Of the elements of the ventral shield, two are median and symmetrical, four lateral and in pairs. The two latter, upon each side, are broad at their remote ends and narrower at their adjacent ends, whose outer edges are, besides, somewhat bent up. Of the median plates, the posterior is rhomboidal and articulates with all the others; the anterior has the form of an elongated isosceles triangle, whose base, directed anteriorly, is rounded off and forms the middle of the anterior margin of the ventral shield.

The stout, doubly curved, clavicle-like bones Mn., found, in complete specimens, on the under side of the head, have one edge beset with minute denticles for a short distance; and there are two other flat, elongated, bones, devoid of sculpture upon their outer surfaces, which lie between them and the anterior edge of the ventral shield.

Beside the parts now described, the only other bones known to belong to *Coccosteus* are the neural and subcaudal arches, the fin-rays and their supports, and the curved ossicles which lie just behind the body armour, and were perhaps connected with ventral fins; but I enter into no particular description of these, as they are not essential to my present purpose.

For some years past I had suspected that the modern Siluroids presented more analogies to the seemingly aberrant Devonian fishes than any other members of the class Pisces, and from the examination

of dried specimens, I had even pitched upon the Siluroid genus *Clarias* as that most likely to help me to understand *Coccosteus*; but it was not until my friend and former pupil, Mr. J. J. Monteiro, brought home for me from Congo some specimens of *Clarias capensis* preserved in spirits, that I was able to examine the osseous structure of that fish with sufficient care and thoroughness for the purposes of an efficient comparison.

In fig. 20 a careful, reduced representation of the top of the skull of this fish is given, and it will be seen that, in everything but the minor details of form, it agrees with *Coccosteus*. The middle line of the skull is, as in the latter genus, occupied by three bones. S. O., the supra-occipital, is, in the recent form, pointed behind; Fr., the principal frontal, is, as in the fossil, four-rayed; it exhibits a considerable gap or fontanelle, but no median suture; Eth., the ethmoid, and Pmx., the premaxilla, correspond exactly in the two skulls, if we leave out of consideration the position of the suture seen in the fossil in this region. The bone Pr. F., which can be at once identified as the prefrontal in *Clarias*, and which sends down a process dividing the orbit from the nostril, obviously corresponds with the similarly related bone in *Coccosteus*; while in *Clarias* the orbit is completed below by the spatulate suborbital bone, Sb. O., smaller in proportion and undivided, but otherwise similar to the bone *z*, *z'* of *Coccosteus*. The post-orbital bone, Pt. O., and the supra-temporal bone, S. T., of the former appear to have their homologues in the bones *x* and *y* of the latter fish.

The space between the frontal, the supra-occipital, and the supra-temporal is occupied, in *Clarias*, by two bones, the anterior of which certainly represents the post-frontal; while the posterior occupies the situation of no less than three distinct bones in the heads of ordinary fishes, viz., the parietal, the squamosal, and the epiotic. The reduction in the normal number of bones which obtains in the Siluroid has been carried a step further in *Coccosteus*, where the plate lettered for shortness' sake only Pa. Ep. is the only representative of the bones Pt. F. and Pa. Sq. Ep. of *Clarias*.

Lastly, comes the bone S.s. naturally united in *Clarias* to Pa. Sq. Ep. and to S. T., and which corresponds with the supra-scapula of ordinary osseous fishes, in which it is usually connected with the skull only by ligament. The Siluroids and Ganoids, however, coincide in always having this bone more closely united with the regular cranial bones, and *Coccosteus*, it will be observed, agrees with them.

So much for the cranial shield. To comprehend the dorsal and ventral body shields we must have recourse, not to *Clarias*, but to other Siluroids, such as *Bagrus*, *Arius*, &c. In these fishes, in fact, the an-

terior dorsal interspinous bones become so modified as to form a great shield-shaped dermal plate, with a strong inferior crest, which occupies the same position and has the same relations as the medio-dorsal plate of *Coccosteus*, though it commonly bears a strongly articulated spine, which is absent in the latter genus. In some species, as *Arius cruciger*, the principal plate is provided with lateral accessory plates, in which, perhaps, we have the homologues of the dermal plates *b*, of *Coccosteus*. It is possible that *c* may have been the operculum, which occupies a nearly similar position in *Arius*, but if it were suturally connected with

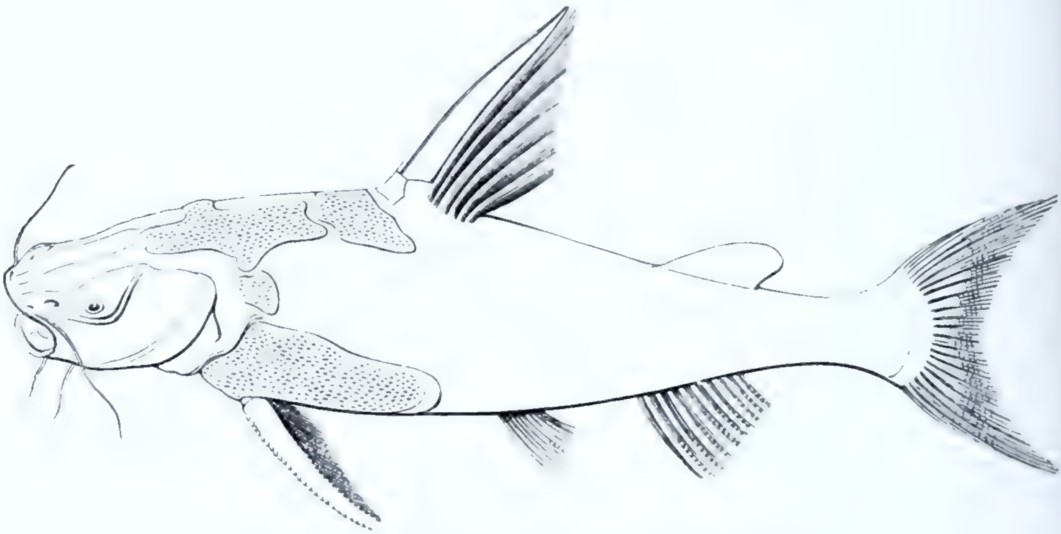


Fig. 20A. *Arius rita*, after Cuvier and Valenciennes.

the suprascapula, this view would be untenable, and the bone would have to be regarded as a scapular element.

In the Siluroids to which I have referred, and in *Loricaria*, a vast latero-ventral shield is produced by the prodigious expansion and coalescence of the bony elements which are homologous with those termed "coracoid" and "radius" in other fishes. Viewed from the ventral surface, these bones form four great plates, those of each side being closely united, or even amalgamated together, while the opposite pairs are joined, in the middle line, by a strongly serrated suture.

When the pectoral fin is provided with an anterior spine, this is articulated by a curiously complicated joint with the so-called coracoid. The cornua of the hyoid are large stout bones, and the urohyal, also a large and strong bone, which is particularly broad in *Loricaria*, connects the hyoidean with the pectoral apparatus.

On comparing this apparatus with the sternal shield of *Coccosteus*, one is tempted to compare the antero-median piece of the latter with

the urohyal of the Siluroid, the antero-lateral piece with the "coracoid," and the postero-lateral piece with the so-called "radius," the more especially as the antero-lateral piece corresponds with that part of the thoracic shield of *Pterichthys* which supports the plated appendage representing the pectoral fin, in that genus.

On the other hand, it must be confessed that the closer connexion of the antero-median piece with the thoracic plates than with the hyoidean cornua, and the very backward position of the postero-lateral plates, apparently out of reach of any connexion with the fins, militate against this view; which, in addition, leaves the median rhomboidal plate unaccounted for.

The bones Mn. are, of course, as has long been determined, the rami of the mandibles of *Coccosteus*. Their singular figure is not unlike that of the corresponding bones in *Loricaria*. Finally, the long

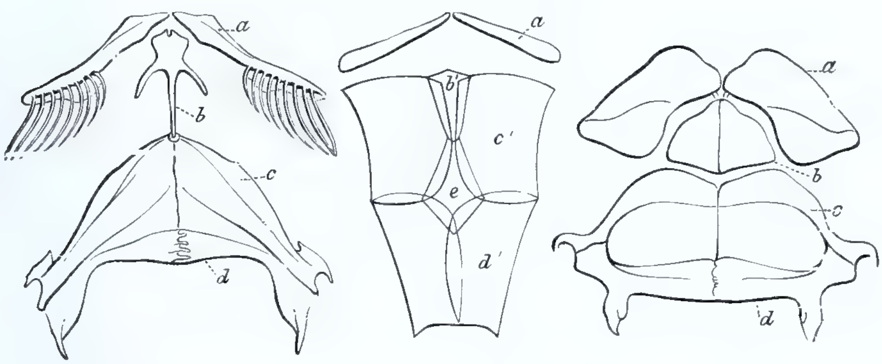


Fig. 21. Hyoidean and Pectoral Plates of *Clarias*, *Coccosteus*, *Loricaria*.

flat bones *a* (fig. 21), I have no doubt, are the chief parts of the hyoidean arch, which are also proportionately large in many Siluroids.

No one, I think, will deny that the structural coincidences here detailed are of very great weight, and that in the absence of contrary evidence they must lead us to assign a place near, if not among, the Siluroidei to *Coccosteus*. I do not know that any facts which can be adduced can be fitly considered as such directly contrary evidence, but there are several difficulties which require careful consideration.

In the first place, *Coccosteus* seems to have possessed neither basal nor lateral cranial bones,—at least, no traces of such structures have yet been discovered; so that, in all probability, this fish possessed a cartilaginous primordial cranium like that of *Accipenser*; and, indeed, a still more gristly one, for *Accipenser* has a large basal ossification. The hyomandibular suspensory apparatus must have been equally cartilaginous, and, in the vertebral column, only the superior and in-

ferior arches were ossified. Assuredly this is very unlike what we are accustomed to see among the Teleostei, but it must be recollected that it is at least equally unlike what we find in the Ganoids, if we except those of the same epoch; and, on the other hand, there are some recent Teleostei, though there are no known Ganoidei, whose vertebral columns and skulls exhibit a correspondingly low stage of organization.[1]

In the second place, arises the question whether, since we know that a true Ganoid, *Amia*, completely simulates the outward form of a Clupeoid Teleostean, while retaining all the essentials of its order,—may not *Coccosteus* be also a true Ganoid which simulates the outward aspect of a Siluroid? To this question it is, perhaps, impossible to give any answer, save by asking another, viz.:—Why should not a few Teleosteans have represented their order among the predominant Ganoids of the Devonian epoch, just as a few Ganoids remain among the predominant Teleosteans of the present day? When it is considered that an ichthyologist might be acquainted with every fresh-water and marine fish of Europe, Asia, Southern Africa, Southern America, the Indian Archipelago, Polynesia, and Australia, and yet know of only one Ganoid, the Sturgeon, a fish so unlike the majority of its congeners, that a naturalist might be well acquainted with almost all the fossil Ganoids, and yet not recognize a sturgeon as a member of the group,—it will not seem difficult to admit the existence of a Teleostean among the Devonian Ganoids, even though that Teleostean should in some, even important, points differ from those with which we are familiar.

At any rate, I think the *primâ facie* case in favour of the Teleostean nature of *Coccosteus* is so strong, that it can no longer be justifiable to rank it among the Ganoids, "*sans phrase*," but that even those who will not allow it to be Teleostean must attach to it the warning adjunct of *incertæ sedis.*

No one doubts that wherever *Coccosteus* goes, *Pterichthys* must follow, and though the structure of the last-named fish is, in some respects, more difficult of interpretation than that of the former, in others it is strikingly Siluroid. For example, I know of no piscine structure that is even remotely comparable to the proximal joint of the pectoral limb of Pterichthys, except the corresponding articulation of the pectoral spine and fin of the Siluroids. And again the example of *Ostracion* shows that the box-like cincture of the body of *Pterichthys* is by no means foreign to the Teleostean group, though it cannot be paralleled by fishes of any other order. Whether the other "Placodermi"

[1] See on this point, however, the remarks at p. 457 under (3).

of Pander, such as *Asterolepis* (Ag. and Miller) really belong to the same group as *Coccosteus* and *Pterichthys*, or not, is a question which can perhaps be hardly settled at present ; although, provisionally, I am much inclined to associate them together. In principle, the cranial structure of *Asterolepis* is very similar to that of *Coccosteus*.

Having disposed of the undoubted Elasmobranchs, of the Crossopterygian Ganoids, and of the "Placodermi" of the Devonian epoch, several important and rather difficult groups remain for discussion. These are the Acanthodidæ, the genera *Cephalaspis* and *Pteraspis*, and the genus *Cheirolepis*.

The ACANTHODIDÆ have hitherto been ranked among the Ganoids, but the following considerations have often led me strongly to suspect that they might be Elasmobranchs : —

1. Their dorsal spines are similar in form and mode of implantation to those of the Elasmobranchii, except perhaps that the surface of the implanted portion is less different from the rest than in the latter order.

2. Their dermal ossicles are more like shagreen than scales.

3. As Roemer has pointed out, their lateral line runs between two rows of these ossicles, and is not formed by separate canals or grooves in successive scales as in most Ganoids and Teleosteans.

4. They seem to have had no distinctly ossified cranial bones.

5. They have no opercular apparatus, but as Sir Philip Egerton long ago pointed out to me, their branchial arches are naked.

6. The sternal part of their pectoral arch seems to have had no bony connexion with the head.

On the other hand, however, it must be considered that,—

1. The Acanthodidæ, unlike all Elasmobranchs, have great spines articulated with the pectoral arch.

2. The dermal plates of the Ganoid *Cheirolepis* are very shagreen-like, though affirmed by Pander to differ in structure from those of Acanthodidæ.

3. The cranial bones become less and less developed in the Chondrosteous Ganoids, until in *Spatularia* they are very thin squamose lamellæ ; so that there is no great difficulty in the way of supposing their entire absence in a true Ganoid.

4. In the same way, the opercular apparatus, small in *Accipenser*, is still more reduced in *Spatularia*.

5. The thin, curved, toothless mandibles of *Spatularia* present, perhaps, the nearest analogue to the singular mandibular bones of *Acanthodes*.

6. As Roemer has pointed out, *Paleoniscus* has orbital plates very like those of *Acanthodes*.

7. The production of the pectoral arch into long backwardly directed processes in *Diplacanthus* and *Cheiracanthus* is the very reverse of an Elasmobranch character, seeing that the like only obtains, so far as I know, in some Siluroids.

8. *Acanthodes* is provided with two very long filaments, beset with short lateral branches, which proceed from the region of the mouth, and such oral tentacles are to be found only in Ganoids and Siluroids.

Under these circumstances the safest course probably is to regard the Acanthodidæ as a distinct suborder of Ganoids.

The genera *Cephalaspis*, *Pteraspis*, *Auchenaspis*, and *Menaspis* certainly form a family by themselves, to which the title of CEPHALASPIDÆ may be conveniently applied; but the position of this family is not readily determinable. No one can overlook the curious points of resemblance between the Siluroids, *Callichthys* and *Loricaria*, on the one hand, and *Cephalaspis*, on the other, while in other respects, they may be still better understood by the help of the Chondrostean Ganoids. Compare, for example, *Scapirhynchus* with *Cephalaspis*, or the great snout of *Pteraspis* with that of *Spatularia*. I am inclined to place the Cephalaspids provisionally among the Chondrostei, where they will form a very distinct family.

The affinities of two genera remain for discussion, the one being the well-known *Cheirolepis* of Agassiz, the other, the new genus *Tristichopterus*, described by Sir Philip Egerton in the course of the following Decade.

Cheirolepis contains fishes with moderate-sized heads and markedly heterocercal tails; with a single dorsal fin, a single anal, pectorals, and ventrals. The median fins are situated forwardly, the dorsal being over the posterior part of the anal; and the ventral fins are so forward as to be almost close to the pectorals. None of these fins are lobate. The body is covered with minute rhomboidal scales, which do not overlap one another, so that the skin has quite the aspect of shagreen. Nevertheless, according to Pander, the structure of these bony scales is not so like that found in the Squalidæ as that of the scales of *Diplacanthus*.

The head is usually crushed, and its component elements displaced, but according to Professor Pander, whose account is largely borne out by the specimens I have examined, the middle of the roof of the cranium, from the posterior edge of the occiput to the anterior

edge of the frontal region, is covered by two broad bony plates, which were, perhaps, divided in the middle line. Pander considers the anterior of these to be frontals, the posterior to be parietals. At the sides of the parietals lie three narrow bones, which, perhaps, all belong to the skull, though the inner and uppermost may appertain to the shoulder girdle. The anterior edges of the other two bound the orbit posteriorly, and similarly elongated plates lie in front of the eyes, beside the frontals. The upper jaw is a large bone, rounded off posteriorly, and tolerably broad behind, while anteriorly its upper edge suddenly becomes excavated to form the lower boundary of the orbit and then tapers off; it is beset with small sharp conical teeth. The gape extends very far back, and the lower jaw is a long flat bone toothed like the upper.

According to Agassiz, there were larger teeth interspersed among the smaller ones ("Recherches," p. 130; "Vieux Grès Rouge," p. 44), but all in a single row. Like Pander (l. c., p. 73), I have been unable to discover these larger teeth. The opercular apparatus and the branchiostegal rays, or their representatives, were not observed by Pander, nor have I seen indubitable evidence of their characters; but Agassiz ("Recherches," p. 132) has described and figured the branchiostegal rays of *Ch. Uragus.* "The branchiostegal rays are very well preserved on both sides of the head; the anterior are shorter and larger; they are well seen on the left side. The posterior ones, which are better preserved on the right side, are narrower and more elongated. I count at least ten of them."

According to Pander a large perforated plate surrounds the eye.

Miller, Giebel, and Pander have agreed upon the propriety of separating *Cheirolepis* from the other Acanthodidæ of Agassiz, and Pander proposed to form for it a distinct family, that of the CHEIROLEPINI. Granting, as I think every one must do, the justice of this step, the question next arises in what suborder of the Ganoids does this family arrange itself.

It certainly is not one of the Crossopterygidæ, for it has but a single, comparatively short, dorsal fin, neither pectorals nor ventrals are lobate, and there are no jugular plates; still less can *Cheirolepis* be ranked among the Amiadæ or Chondrosteidæ. On the other hand, it presents certain points of resemblance with *Paleoniscus*, and through those forms connects itself with that large body of fossil fishes which have more or less direct relations with *Lepidosteus.* Perhaps then, *Cheirolepis* ought to be regarded as the earliest known form of the great suborder of the Lepidosteidæ.

In the absence of a full knowledge of the head, of the paired fins

and of the dentition, it would be hazardous to form any decided opinion as to the affinities of *Tristichopterus* ; I strongly suspect, however, that it will turn out to be the type of a new family allied to the Ctenododipterini and Cœlacanthini.

The cranio-facial bones are lettered as follows in the woodcuts :—

S. O. Supra-occipital.
Fr. Frontal.
Eth. Ethmoid.
Ep. Epiotic.
Pa. Parietal.
Sq. Squamosal.
Pt. F. Post-frontal.
Pr. F. Pre-frontal.
S. T. Supra-temporal.
Pt. O. Post-orbital.
Sb. O. Sub-orbital.
Mx. Maxilla.
Prmx. Premaxilla.
H. M. Hyomandibular bone.
Qu. Os quadratum.
S. S. Supra-scapular.
Op. Operculum.
S. Op. Sub-operculum.
Ju. Jugular bones.
Sp. O. Spiracular ossicles.
St. O. Supra-temporal ossicles.

P.O. "Pre-operculum" occurs in the woodcut, fig. 2. ; but I am now much inclined to doubt the existence of a true pre-operculum in any Crossopterygian fish.

Jermyn Street, Nov. 1, 1861.

[NOTE.—By the great kindness of Dr. Taylor, of Elgin, I have just had the opportunity of examining a beautiful, almost entire, specimen of *Glyptopomus*, with two dorsal, and exquisitely lobate pectoral, fins.—T. H. H., Nov. 18th.]

XXIV

GLYPTOLÆMUS KINNAIRDI

Memoirs of the Geological Survey of the United Kingdom. Figures and Descriptions illustrative of British Organic Remains. 1861, *Decade X.*, *pp.* 41–46.

PLATES I. AND II. [PLATES 33 AND 34].

[Genus GLYPTOLÆMUS. HUXLEY. (Sub-kingdom Vertebrata. Class Pisces. Order Ganoidei. Suborder Crossopterygidæ. Family Glyptodipterini.) Body elongated, tapering to a point posteriorly. Cranium depressed. Dorsal fins, two, distinct, situated in the posterior two-fifths of the length of the body. Ventral fins under the first dorsal, and like the pectorals lobate. The rhomboid scales and the cranial and facial bones ornamented with raised ridges. Teeth of two sizes, composed of (probably) dendrodentine. Tail diphycercal.]

Glyptolæmus Kinnairdi. SP. UNICA.

SPECIMENS of this genus were first described, and their distinctive characters pointed out by me, in a notice inserted in Dr. Anderson's work upon "Dura Den," which was accompanied by excellent, though small, illustrative figures, drawn by Mr. Dinkel.

Since 1859, thanks to Dr. Anderson's zeal and activity, a number of additional specimens, several of great beauty and interest, have passed into the collection of the Museum of Practical Geology, so that I am now in a position to give a tolerably complete account of the structure of these ancient fishes. The singularly beautiful and accurate figures in Plates I. and II. [Plates 33 and 34] will enable the reader, step by step, to verify for himself the most important points of my description.

The body is, as I have said, elongated, and when viewed side-ways, fusiform, tapering to a point at each extremity (Plate I. [Plate 33] fig. 1) but when viewed from above or below, though the caudal extremity is still seen to end in a point, the anterior part of the body rapidly widens (Plate I. [Plate 33] fig. 3), and ends in a depressed, broad, and shovel-shaped head, with a semi-elliptical contour, rounded at the snout.

The length of the whole body is about four and a half times as

great as the distance from the end of the snout to the posterior margin of the opercular apparatus ; which distance exceeds by as much as a fourth, or a fifth, the transverse diameter of any part of the body. It somewhat exceeds, again, the perpendicular distance from the upper margin of any part of the dorsal, to the lower margin of any part of the anal fin. The greatest transverse diameter of the head is equal to the distance from the snout to the posterior margin of the parietal bones.

The specimen figured in Plate II. [Plate 34] furnishes a very complete view of the structure of the cranium of *Glyptolæmus*, the arrangement of whose constituent elements is still further elucidated by the diagrammatic woodcuts fig. 2 (p. 2 of the "Preliminary Essay"), made from enlarged and restored views of the skull and its appendages.

The cranial bones are thin and scale-like, and their surface exhibits numerous long and sinuous ridges, separated by narrow and comparatively deep grooves, which sometimes obscurely radiate from the centre of the bone.

The premaxillary bones, slender and slightly curved, uniting in a broad, but short, ascending internasal process, form the anterior boundary of the snout and limit the nostrils below, joining the equally slender maxillaries which constitute the rest of the upper boundary of the gape behind. The upper and inner edges of the ascending processes of the premaxillaries abut against the anterior margins of a flat hexagonal bone, whose posterior margins unite with the frontals, while its lateral edges are connected with the inner edges of the nasal bones. This bone is therefore obviously the ethmoid.

The frontals, which succeed the ethmoid in the middle line are short, but comparatively narrow bones, separated by a very distinct suture, which widens in the middle of its length, so as to form a small rhomboidal fontanelle. The posterior edges of the frontals are truncated, and unite with the anterior margins of the parietals, which are almost twice as long as the frontals, and enter more largely than any other bones into the formation of the roof of the skull. The left parietal rather overlaps the right posteriorly, and each parietal suddenly widens in its posterior moiety, so that its outer edge presents a deep notch or step into which the post-frontal fits. The posterior edges of the parietals are as abruptly truncated as the anterior. They unite in the middle line with the apex of the large rhomboidal scale, or bone, which occupies the place of the supraoccipital.

The supero-lateral regions of the skull are formed in front by the large nasals ; behind these by the prefrontals, which unite with the

maxilla, the nasals and the frontals below, in front and above, and apparently, with the post-frontal behind. Their posterior excavated margins form the anterior boundary of the orbit.

The post-frontals, better defined posteriorly than anteriorly, appear to join the prefrontals, and then, extending backwards beyond the posterior margins of the frontals, they unite with the anterior moiety of the parietals, filling up all that notch in the outer border of these bones, which has been described. Their posterior edges are connected, internally, with the anterior margins of the projecting part of the parietal, externally with the same margins of the small quadrilateral squamosal bones.

The posterior part of the supero-lateral region is completed by two squamiform bones, which take the place of the external occipital, or epiotic, bones of other fishes, filling the interspaces left between the supraoccipital and the opercular apparatus. The inner surface of this bone, on the left side, presents a very well marked triradiate impression, one crus of which is directed transversely inwards, while the others are respectively directed forwards and backwards. A shallow groove upon the surface of the supraoccipital, which has a slight concavity forwards, connects the transverse crus of the impression on one of these bones with that on the other.

The triradiate marks are much more distinct upon the inner surface of these bones, where they form distinct ridges, than upon the outer surfaces, where they appear only as very shallow and indistinct grooves; and, except for the continuation of each transverse crus into its fellow across the supraoccipital, I should have been disposed to connect them rather with the semicircular canals of the auditory organ than with the so-called mucous grooves.

The lateral regions of the skull behind the premaxillaries are formed, in front of the orbit, by the prefrontal and maxillary, and behind the orbit, first, by the maxilla and a large postorbital bone, then by the maxilla, by the bone marked P. O., which may very likely not be a true preoperculum, and a large supratemporal bone. The latter articulates above with the postfrontal and squamosal, and fits posteriorly into the notch formed by the vertical and horizontal portions of the bone P. O.

The operculum, a large four-sided bony plate, is connected with the outer edge of the epiotic above and with the posterior edge of the ascending ramus of the bone P. O. in front. Its lower edge articulates with the upper margin of the suboperculum, which is about half as large as the operculum, and has a much more rounded posterior edge,

The palato-quadrate arcade is best exhibited in fig. 1a, Plate I.

[Plate 33] though the lines of demarcation between its constituents are not visible. Posteriorly, it is broad and expanded, furnishing the condyle to the mandibles by its outer and lower margin, while its upper and inner part probably abutted against the sphenoid. Anteriorly, it rapidly narrows, and is continued forwards as a strong bony bar. Running parallel with and outside this, is a second elongated bony ridge, which may be distinct from the foregoing, or may be only the outer part of it. At any rate, the two seem to become one in front. Here they support a very strong tooth, and there is a second large tooth situated far back upon the outer bone.

This palato-quadrate apparatus, taken altogether, very much resembles that of *Lepidosteus* in form, and in the large teeth which it bears.

The contour of the stout mandible follows that of the head, the gape extending as far back as the level of the posterior edges of the parietal bones. The rami are very stout, but appear to have consisted of only a thin osseous shell, sculptured externally in the same way as the cranial bones. The constituent elements of the mandible are not distinctly separated from one another in any specimen.

The jugular plates consist of two principal and a number of lateral scale-like bones. The former are elongated, nearly right-angled, triangles, with their perpendiculars turned towards one another, and their apices engaged in the re-entering angle of the rami, while their bases are situated midway between the articular ends of the rami and the posterior margins of the opercular apparatus. The peculiar sculpturing of these plates gave rise to the name of the génus, and is well shown in fig. lv, Plate II. [Plate 34]. The outer edges of the principal jugular bones lie close to the inner edges of the rami of the mandible anteriorly, but posteriorly a space is left between them, which gradually widens posteriorly, and is so continued between the suboperculum and the posterior part of the principal jugular plate. This interval is filled up by the secondary jugular plates, of which, in one specimen, I count five, gradually increasing in size from before backwards. All these plates exhibit the characteristic surface ornamentation, and the last, much larger than any of the others, extends beyond the level of the posterior margin of the principal jugular plate, its curved free margin sweeping backwards and outwards, and lying between the suboperculum and the pectoral arch, while a considerable portion of the bone seems to pass under and be overlapped by the suboperculum. There is no median rhomboidal intercalary bone between the anterior and inner edges of the principal jugular bones.

The ventral part of the pectoral arch is represented, on each side, by two broad, triangular, somewhat curved, bones. The anterior one

meets its fellow in the middle line, just behind the posterior edges of the principal jugular bones ; but their inner margins immediately diverge, passing backwards and outwards, and being continued in the same direction as far as the posterior edge of the operculum, by the inner edge of the posterior pectoral plates. The adjacent margins of the two plates seem to be firmly united together, and their outer surfaces exhibit a marked sculpture, whose ridges are more evenly continuous than those of the cranial bones. Two large triangular scales which fit in between the supraoccipital and the epiotic appear to represent some of the upper elements of the pectoral arch.

The pectoral fins are not perfectly displayed in any specimen, but fig. 2, Plate II. [Plate 34], shows that they were well developed, being about as long as the head, and that they were provided with numerous long and delicate fin rays which beset the edges and extremity of a stout central stem, covered with rhomboidal scales.

The ventral fins, smaller than the pectorals, were also, as figs. 2, 3, Plate I. [Plate 33], show, distinctly lobate, their central stem being covered with rhomboidal scales and terminating in a point, at about the middle of the length of the fin.

The median fins present very distinct jointed fin-rays, and, as may be seen in fig. 1, Plate I. [Plate 33], the scales of the body are continued on to the bases of the dorsals and anal, so as to give them, though to a far less degree, the lobate aspect of the pectorals and ventrals.

Both dorsals are pointed at their extremities, and somewhat fan-shaped, from being narrower at their bases than in their posterior moieties. The first dorsal is smaller than the second. The anal fin, opposite the second dorsal, is about as large as the latter, and has the same slightly lobate aspect.

The rhomboidal caudal fin, whose rays commence almost immediately behind those of the second dorsal and anal, is perfectly symmetrical, the axis of the tapering extremity of the body being not only free from any upward inflexion, but corresponding with the "equator" of the fin.

The scaly extremity of the body appears to stop at some distance before reaching the posterior margin of the fin, but it is difficult to make quite sure of the fact.

The scales are thin, and exhibit a sculpture of variable appearance, but always made up of raised ridges, with intervening valleys and pits over the greater part of their surface ; narrow smooth facets being left along two sides to receive the overlapping edges of other scales.

A single longitudinal row of hexagonal scales occupies the middle line of the back, and a less marked row of rhombic scales runs along

the ventral median line. The lateral scales, rhomboidal in form, extend from the medio-dorsal to the medio-ventral series, forming curved rows transverse to the axis of the body in general direction, but presenting a marked concavity, or re-entering angle, forwards.

With respect to the dentition of *Glyptolæmus*, I find a series of minute pointed teeth along the outer margins of both upper and lower jaws. Besides these there is a single large tooth upon each side of the symphysis of the mandible, and at least one more of the same kind, a little in front of the middle of the ramus (fig. 1 b, Plate II. [Plate 34]). In the upper jaw, the pterygopalatine apparatus is, as I have already pointed out, provided with several similar teeth.

Glyptolæmus is at present only known to occur in the Old Red Sandstone of Dura Den.

EXPLANATION OF PLATES I. AND II. [PLATES 33 AND 34.]

Plate I. [Plate 33.]

Fig. 1. Side view of a specimen of *Glyptolæmus Kinnairdi*, half the size of nature. This and the other figures of the plate are taken from specimens in the Museum of Practical Geology.

Fig. 1a. Head of the same, natural size.

Fig. 2. Ventral and anal fins of another specimen.

Fig. 3. Ventral view of another specimen, half the natural size. Mus. Pract. Geol.

Fig. 4. Scales magnified.

Plate II. [Plate 34.]

The figures give various views of a specimen of *Glyptolæmus Kinnairdi* in the Museum of Practical Geology, and are all, except 3, 4, and 5, of the natural size.

Fig. 1. Dorsal view of the body.

Fig. 1a. Lateral view of the head.

Fig. 1b. Front view of the head.

Fig. 1c. Ventral view of the body.

Fig. 2. Sandstone matrix into which the body fits, and which retains many of the dorsal scales and the pectoral fins.

Figs. 3, 4, and 5. Scales from different parts of the body magnified.

November 1, 1861.

Geological Survey of the United Kingdom.

Fig 1

Fig 1a

Fig 2

Fig 4

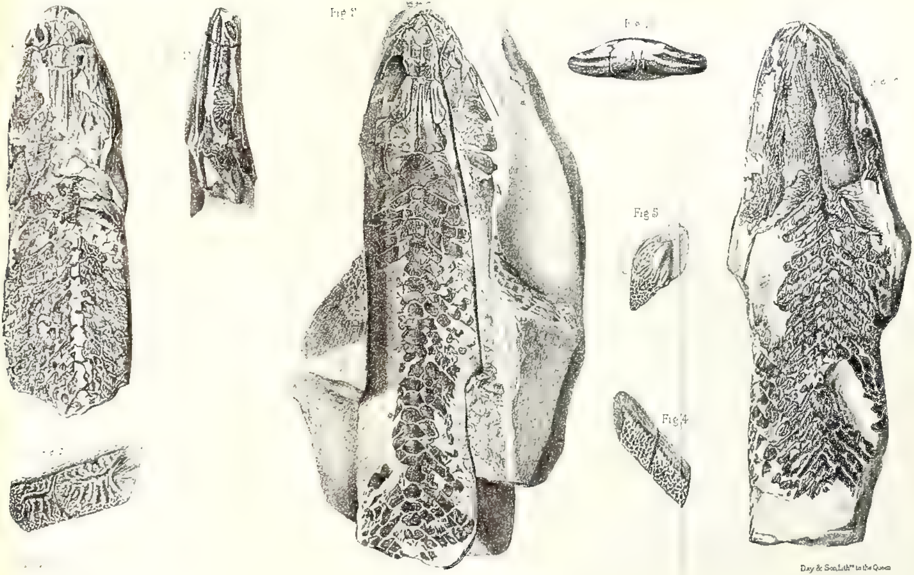
Fig 3

Day & Son Lith^rs to the Queen

GLYPTOLŒMUS KINNAIRDI. *Huxley*

Geological Survey of the United Kingdom.

GLYPTOLŒMUS.



Day & Son Lith^rs to the Queen

GLYPTOLŒMUS KINNAIRDI. *Huxley*

XXV

PHANEROPLEURON ANDERSONI

Memoirs of the Geological Survey of the United Kingdom. Figures and Descriptions illustrative of British Organic Remains., 1861, *Decade X.*, *pp.* 47–49.

PLATE III. [PLATE 35].

[Genus PHANEROPLEURON. HUXLEY. (Sub-kingdom Vertebrata. Class Pisces. Order Ganoidei. Sub-order Crossopterygidæ. Family Phaneropleurini.) Body elongated, tapering to an acute point posteriorly, compressed from side to side. Dorsal fin single, extending for nearly the length of the posterior half of the body; the paired fins acutely lobate; the ventrals very long, apparently longer than the pectorals, and situated beneath the anterior end of the dorsal fin. Tail inæquilobate, the upper lobe being by far the smaller. Scales cycloid, very thin. Teeth numerous and conical. Neural arches, ribs, and interspinous bones well ossified.]

Phaneropleuron Andersoni. SP. UNICA.

ALL the specimens of this species and genus at present known have been procured from the Old Red Sandstone at Dura Den, associated with *Holoptychius*, the two genera being constantly found associated in the same slabs of sandstone. A fine series of examples is to be seen in the British Museum and the Museum of Practical Geology, the whole of which, I believe, were collected by Dr. Anderson, in whose work upon Dura Den the first description of the present species appeared. The fish had received the name of *Glypticus* from Agassiz long before, but the name was unaccompanied by any description or definition, and has been used for a genus of Echinodermata. The most complete specimen I have seen is that figured (two-thirds of the natural size) in Plate III. [Plate 35] fig. 1, which occurs among a number of other examples of this genus and of *Holoptychius*, in a fine slab marked 26120 in the collection of the British Museum.

The length of body equals about $5\frac{1}{2}$ lengths of the head. It remains of tolerably equal thickness from the pectoral region to that of the ventral fins, and then gradually tapers off to a finely pointed caudal extremity, which is, usually, slightly bent upwards. When the mouth is shut, the head also presents a triangular contour, both its upper and its under outlines rapidly shelving towards the snout.

The scales are exceedingly thin, and, apparently in consequence of containing very little bony matter, they are apt to run into one another and lose their distinctness when fossilized. But so far as the best preserved specimens enable me to judge, they were large and circular, and their outer surfaces were marked by very slight and delicate, granular, radiating striæ, which may, however, be indications of internal structure and not of ornamentation (Pl. III. [Plate 35] fig. 7). These differences from the scales of *Holoptychius* become particularly obvious when, as in the slab in the British Museum above referred to, specimens of the two genera lie side by side in the same matrix, or when, as in fig. 3, Plate III. [Plate 35], detached scales of *Holoptychius* have become imbedded in the midst of a specimen of *Phaneropleuron*.

The cranial bones are smooth, or, at most, present irregular and scattered grooves. The cranium seems to have been much more compressed from side to side than in most Devonian fishes, but I can say little else respecting its structure, as it is much injured in all the specimens I have seen. In no specimen are the boundaries of the cranial bones defined. The operculum, however, is large. The orbit seems to have been situated far forwards, and the gape is long. Both the upper and the lower jaw are beset with a single series of sharp short conical teeth. One specimen on the slab 21620 in the British Museum exhibits the only view of the under surface of the head I have met with, and proves that the jugular region was protected by bony plates. Whether there were more than the two principal ones, or not, however, I cannot make out with certainty.

The pectoral arch is well developed, but I can say nothing as to its individual components, nor are the pectoral fins thoroughly well preserved in any specimen. Such parts of them as exist lead me to the belief that they were shorter than the ventrals, but like them acutely lobate.

No pelvic bones are discernible, but the ventral fins are beautifully displayed in two examples on the slab 26120 in the British

Museum, and in another specimen marked 26117 in the same collection.

Their length exceeds the greatest vertical diameter of the body. A taper central lobe extends through the whole length of the fin, ending in a point at its fine end. It is covered throughout with cycloid scales, having the same characters as those of the body, and both edges are fringed with delicate fin-rays.

The notochord was persistent throughout the whole length of the vertebral column, while the superior and inferior arches were well developed and thoroughly ossified.

The neural spines are long, and are curved, so as to be somewhat concave forwards and upwards. In the posterior moiety of the body, elongated interspinous bones, narrow in the middle and expanded at the ends, are adapted to them. These interspinous bones increase in length from before backwards to beyond the middle of the dorsal fin, and support the fin-rays whose bases are broad and solid, while they divide into a series of branchlets at their ends. There may be more than one fin-ray to each interspinous bone.

The dorsal fin, commencing with the posterior half of the body, gradually increases in height posteriorly, as its upper margin remains parallel with the axis of the body, while the dorsal line of the body converges towards that axis; the fin terminates posteriorly in an almost vertically truncated extremity.

The ribs attain a considerable length, even close to the head, and are continued through the whole length of the abdomen, passing gradually into the subcaudal bones. They are well ossified, and hence, in the fossil state, they stare through the thin integumentary scales of the fish so as to suggest its generic name.

The anal fin is somewhat lanceolate in shape, inclined downwards and backwards, and so long that its lower extremity is as distant from the axis of the body as the upper edge of the dorsal. It is supported by interspinous bones like those of the dorsal fin.

The inferior lobe of the caudal fin commences immediately behind the anal, and its rays appear to be supported by similar interspinous bones, at least anteriorly. It can be traced backwards to near the extreme end of the body. The superior lobe, on the other hand, seems to have been obsolete.

EXPLANATION OF PLATE III. [PLATE 35.]

Fig. 1. *Phaneropleuron Andersoni*, two-thirds of the natural size. From a specimen in the British Museum, No. 26,120.

Fig. 2. Head of a specimen in the Museum of Practical Geology. The upper contour of the cranium seems to be slightly distorted. Natural size.

Fig. 3. Caudal extremity of a specimen in the British Museum, exhibiting the anal fin. A scale of *Holoptychius* lies above the end of the tail.

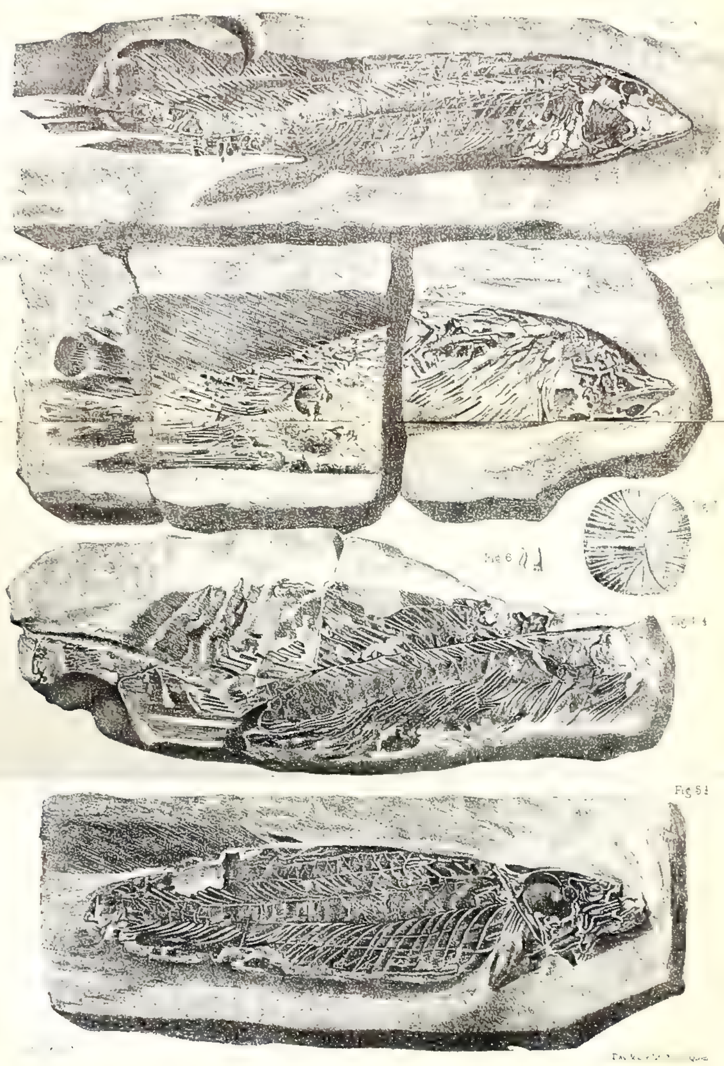
Fig. 4. Hinder part of the body, with ribs, neural arches, interspinous bones, and impression of the caudal part of the tapering notochord. In the Museum of Practical Geology.

Fig. 5. Head and body, with the opercular apparatus and impressions of the ribs and neural arches nearly undisturbed. In the Museum of Practical Geology.

Fig. 6. Teeth magnified.

Fig. 7. A scale magnified.

Jermyn Street, Nov. 1, 1861.



PHANEROPLEURON ANDERSONI *Huxley*

XXVI

ON THE ZOOLOGICAL RELATIONS OF MAN WITH THE LOWER ANIMALS.

The Natural History Review, 1861, *pp.* 67–84.

As the biological sciences have grown in breadth and in depth, and as successive generations of naturalists have succeeded in penetrating further and further into the arcana of nature, the questions—In what relation does the thinker and investigator stand to the objects of his inquiries? What is the tie which connects man with other animated and sentient beings?—have more and more forcibly pressed for a reply.

Nor have responses been wanting; but, unfortunately, they have been diametrically opposed to one another. Theologians and moralists, historians and poets, impressed by a sense of the infinite responsibilities of mankind, awed by a just prevision of the great destinies in store for the only earthly being of practically unlimited powers, or touched by the tragic dignity of the ever-recurring struggle of human will with circumstance, have always tended to conceive of their kind as something apart, separated by a great and impassable barrier, from the rest of the natural world.

On the other hand, the students of physical science, discovering as complete a system of law and order in the microcosm as in the macrocosm, incessantly lighting upon new analogies and new identities between life as manifested by man, and life in other shapes,—have no less steadily gravitated towards the opposite opinion, and, as knowledge has advanced, have more and more distinctly admitted the closeness of the bond which unites man with his humbler fellows.

A controversy has raged between these opposed schools, and, as usual, passion and prejudice have conferred upon the battle far more

importance than, as it seems to me, can rationally attach to its issue. For whether, as some think, man is, by his origin, distinct from all other living beings, or whether, on the other hand, as others suppose, he is the result of the modification of some other mammal, his duties and his aspirations must, I apprehend, remain the same. The proof of his claim to independent parentage will not change the brutishness of man's lower nature ; nor, except to those valet souls who cannot see greatness in their fellow because his father was a cobbler, will the demonstration of a pithecoid pedigree one whit diminish man's divine right of kingship over nature ; nor lower the great and princely dignity of perfect manhood, which is an order of nobility, not inherited, but to be won by each of us, so far as he consciously seeks good and avoids evil, and puts the faculties with which he is endowed to their fittest use.

Important or unimportant in its final results as it may be, however, there can be no doubt that the controversy as to the real position of man still exists ; and I have therefore thought that it would be useful to contribute my mite towards the enrichment of the armoury upon which both sides must, in the long run, be dependent for their weapons, by endeavouring to arrange and put in order the facts of the case, so far as they consist of the only matters of which the anatomist and physiologist can take cognizance—I mean facts of discernible structure and of demonstrable function. If any one assert that there are other orders of facts which enter into this question, but which are distinguished by being neither demonstrable nor discernible, all that can be replied is, that science is incompetent either to affirm or deny his proposition, confined, as she is, to the humble, if safe, region of observation and of logic.

No one denies, I believe, that there are multitudes of analogies and affinities of structure and function connecting man with other living beings. Man takes his origin in an ovum similar in form, in size, and in structure to that whence the dog or the rabbit arise. The physical process which determines the development of the embryo within that ovum ; the successive stages of that development ; the mode in which the human fœtus is nourished within the maternal organism ; the process of birth ; the means provided by nature for the due supply of nutriment after birth : are essentially alike in all three cases. Compare the bony frame-work, the muscles, the great vessels, the viscera, of man, the dog, and the rabbit, and the demonstration of a pervading unity of plan in all three is one of the triumphs of modern science.

The most certain propositions entertained by the human physiologist, those upon which the scientific practice of the healing art depends,

are largely, or wholly, based on the results of experiments on animals. The poison which hurts them does not leave us unscathed; and we share with them two of the most terrible diseases with which mortal beings are afflicted, glanders and hydrophobia. Nor can any impartial judge doubt that the roots, as it were, of those great faculties which confer on man his immeasurable superiority above all other animate things, are traceable far down into the animal world. The dog, the cat, and the parrot return love for our love, and hatred for our hatred. They are capable of shame and of sorrow; and though they may have no logic nor conscious ratiocination, no one who has watched their ways can doubt that they possess that power of rational cerebration which evolves reasonable acts from the premises furnished by the senses—a process, be it observed, which takes fully as large a share as conscious reason in human activity. There is a unity in psychical as in physical plan among animated beings; and the sense of this unity has been expressed in such strong terms by Professor Owen, that his words may form a fitting climax to these introductory sentences.

"Not being able to appreciate or conceive of the distinction between the psychical phenomena of a chimpanzee and of a Boschisman, or of an Aztec, with arrested brain-growth, as being of a nature so essential as to preclude a comparison between them, or as being other than a difference of degree, I cannot shut my eyes to the significance of that all-pervading similitude of structure—every tooth, every bone, strictly homologous—which makes the determination of the difference between *Homo* and *Pithecus* the anatomist's difficulty." [1]

That there are a great number of points of similarity between ourselves and the lower animals, then, appears to be clearly admitted on all hands. It is, further universally allowed that the Vertebrata resemble man more nearly than do any invertebrates; that among vertebrates the Mammalia, and of these the Quadrumana, approach him most closely. Lastly, I am aware of no dissentient voice to the proposition, that in the whole, the genera *Troglodytes*, *Pithecus*, and *Hylobates*, make the closest approximation to the human structure.

The approximation is admitted unanimously; but unanimity ceases the moment one asks what is the value of that approximation, if expressed in the terms by which the relations of the lower animals one to another are signified. Linnæus was content to rank man and

[1] Prof. Owen on the Characters, &c., of the Class Mammalia, "Journal of the Proceedings of the Linnæan Society of London," vol. ii., No. 5, 1857, p. 20, note. It is to be regretted that this note is omitted in the "Essay on the Classification of the Mammalia," which is otherwise nearly a reprint of this paper. I cannot go so far, however, as to say, with Prof. Owen, that the determination of the difference between *Homo* and *Pithecus* is the 'anatomist's difficulty.'

the apes in the same order, Primates, ranging in terms of zoological equality the genera, *Homo*, *Sima*, *Lemur*, and *Vespertilio*. Among more modern zoologists of eminence, Schreber, Goldfuss, Gray, and Blyth, have followed Linnæus, in being unable to see the necessity of distinguishing man ordinally from the apes.

Blumenbach, and after him, Cuvier, conceived that the possession of two hands, instead of four, taken together with other distinctive characters of man, was a sufficient ground for the distinction of the human family as a distinct order—*Bi-mana*.

Professor Owen goes a step further, and raises *Homo* into a subclass, "*Archencephala*," because "his psychological powers, in association with his extraordinarily developed brain, entitle the group which he represents to equivalent rank with the other primary divisions of the class *Mammalia*, founded on cerebral characters."[1]

M. Terres[2] vindicates the dignity of man still more strongly, by demanding for the human family the rank of a kingdom equal to the Animalia or Plantæ; while, finally, a countryman of our own arrogates to his fellows so high a place in the aristocracy of nature as to deny that mankind can be thought of zoologically at all.

From the conception of man as a genus of *Primates* to the refusal to conceive of him as a subject of zoological investigation, is a wide range of opinion—so wide, indeed, as to include all possible views; for in the present state of science, no one is likely to propound the idea that man is only a species of some genus of ape. Ingenious and learned men have held all the doctrines which have been mentioned; great men have held some of them; and, therefore, it is more than probable that the question at issue, if we put the problem in this way, is in reality more one of opinion as to the right method of classification and the value of the groups which receive certain names, than one of fact. But, after all, it is the latter question which really interests science; and, therefore, it seems to me, that some service may be done by setting about the inquiry in a different way—by endeavouring, in fact, to answer the question—What is the value of the differences observed between man and the lower animals, as compared with the differences between the lower animals themselves? Are the differences between man and the apes, for example, as great as those between the ape and the fish? or are they rather comparable to those between the ape and the bird; or, to take a less range, to those be-

[1] Professor Owen on the Characters, &c., of the Class Mammalia, l. c., p. 33.

[2] "L'homme ne forme ni une espèce ni une genre comparable aux Primates. L'homme à lui seul constitue un regne à part—le Regne humain."—Resumé des Leçons sur l'Embryologie Anthropologique, Comptes Rendus, 1851.

tween the ape and the Marsupial; or, to occupy a lower stand still, to those presented by the ape, and, say, the Pachyderm; or, after all, are the differences no greater than those which obtain between different genera of the Quadrumana?

These are questions which can plainly enough be settled independently of all theoretical views. Differences of structure can be weighed by the mind, as definitely as differences of gravity by the balance; nor can any dialectic skill refine them away. It will save trouble, if the attempt be made to answer the last question first—Are the structural differences between man and the Quadrumana no greater than those between the extreme genera of the Quadrumana? If, as I shall endeavour to show, this question can be demonstrably answered in the affirmative;—if it can be proved beyond doubt, that whether we consider the skeleton, the muscles, the brain, or the other viscera, man is far less distant from *Troglodytes* or *Pithecus*, than these apes are from the Lemur, and still more from the *Galeopithecus* or the *Cheiromys*, the other queries will need no separate solution. I have hardly any new facts to bring forward, nor any need to advance such. Thanks to the researches of Duvernoy, Tiedemann, Isidore St. Hilaire, Schrœder van der Kolk, Vrolik, Gratiolet, Professor Owen, and others, all the elements of the problem have long since been determined. It is only necessary to range the admitted facts side by side, in order to show that there is no escape from the conclusion.

And, first, with respect to the differential characters presented by the brains of the chimpanzee and orang from that of man on the one hand, and those of the lowest quadrumana on the other. I begin with this question, because it was my misfortune, at the last meeting of the British Association, to find myself compelled to give a diametrical contradiction to certain assertions respecting the differences which obtain between the brains of the higher apes and of man, which fell from Professor Owen; and in the interest of science, it is well that the real or apparent opposition of competent inquirers, as to matters of fact, should be put an end to as soon as possible, by the refutation of one or the other. Happily, it is unnecessary that I should trust to my memory of what took place on the occasion to which I refer; for the assertions alluded to were already familiar to me, inasmuch as their substance occurs in two of Professor Owen's latest works—the paper "On the Characters, Principles of Division, and Primary Groups of the Class Mammalia," read before the Linnæan Society on February 17th, and April 21st, 1857; and the essay "On the Classification of the Mammalia," delivered as a lecture before the University of Cambridge.

I quote from the former essay, as that intended for an audience

of experts, and hence, in all probability, to be regarded as more strictly scientific :—

"In man, the brain presents an ascensive step in development, higher and more strongly marked than that by which the preceding sub-class was distinguished from the one below it. Not only do the cerebral hemispheres (figs. 5 and 6 A) overlap the olfactory lobes and cerebellum, but they extend in advance of the one, and further back than the other (fig. 6, C). Their posterior development is so marked, that anatomists have assigned to that part the character of a third lobe; *it is peculiar to the genus Homo, and equally peculiar is the posterior horn of the lateral ventricle, and the 'hippocampus minor,' which characterise the hind lobe of each hemisphere.* Peculiar mental powers are associated with this highest form of brain, and their consequences wonderfully illustrate the value of the cerebral character; according to my estimate of which I am led to regard the genus *Homo* as not merely a representative of a distinct order, but of a distinct sub-class of the Mammalia,[1] for which I propose the name of '*Archencephala*' (fig. 6)."

It might be a grave question whether, granting the existence of the differences assumed to distinguish the human brain, they would justify the establishment of a sub-class for the genus *Homo*; but that difficulty is not worth discussing, inasmuch as I shall endeavour to demonstrate, in the course of the following pages, the accuracy of the three counter statements which I made to the audience assembled in Section D, viz. :—

1. That the third lobe is neither peculiar to, nor characteristic of man, seeing that it exists in all the higher Quadrumana.

2. That the posterior cornu of the lateral ventricle is neither peculiar to, nor characteristic of man, inasmuch as it also exists in the higher Quadrumana.

3. That the *Hippocampus minor* is neither peculiar to, nor characteristic of man, as it is found in certain of the higher Quadrumana.

I support the first two propositions by the evidence of every original observer who has written upon the subject, including Professor Owen himself, and by my own personal observations. The third rests upon the evidence of Messrs. Schrœder van de Kolk and Vrolik, and of an eminent countryman of our own, Dr. Allen Thomson, to whom I am indebted for unpublished observations made with express reference to these very points.

1. *The third lobe or posterior lobe of the cerebrum.*—Many anato-

[1] Here occurs the note which I have already quoted at p. 464. The italics in the above extract are my own.

mists divide the cerebral hemispheres of man into only two lobes, the anterior and the posterior, separated from one another by the fissure of Sylvius; but it is more usual to speak of three lobes,[1] an anterior, a middle, and a posterior, the latter, or 'third lobe,' being the posterior, inasmuch as it consists of the hinder part of that, which those who divide the cerebral hemispheres into two lobes, call 'posterior.' It is in this sense that Cuvier, Meckel, and Tiedemann use the term, third or posterior lobe. It is generally admitted that no very strict line of demarcation is traceable between the middle and posterior lobes; anatomists being content to accept Cuvier's curt definition:—

"La partie du cerveau située au-dessus du cervelet est ce qu'on nomme le lobe postérieur du cerveau." [2]

So far as I am aware, the terms "third" or "posterior lobe," have never been applied in any other senses than those which I have indicated. Under these circumstances, it is utterly incomprehensible to me how any one competently informed, either with respect to the literature or to the facts of the case, can assert that the hind lobe "is peculiar to the genus *Homo;*" for not only will the inspection of any ape's brain convince one of the contrary, but the facts were originally ascertained and published by a most competent authority, and have never been doubted for nearly forty years.

Tiedemann's "Icones Cerebrorum Simiarum," published in 1821, in fact, ought to be familiar to every student of mammalian anatomy. On turning to his first Plate, one finds the first figure to be a representation of the brain of "*Simia nemestrina.*" The explanation of the figures says: "*a*, lobus anterior paullulum acuminatus; *b*, lobus

[1] It is not a very easy matter to determine with whom these divisions originated. Vesalius (Humani Corporis Fabrica, libri septem, MDCXLII.) speaks neither of lobes nor of special 'prominentiæ' in the cerebral hemispheres, though he describes them very accurately, explaining particularly that the under surface of these hemispheres is adapted to the 'tubera,' of the cranial bones.

Varolius (Anatomiæ sive de Resolutione Corporis Humani, libri iii., MDXCI. p. 131) says, in his letter to Hieronymus Mercurialis: 'De nervis opticis multisque aliis præter communem opinionem in humano capito observatis;'

"Sunt autem tres cerebri prominentiæ: anterior, media, et posterior . . . . postrema cerebri prominentia replet cavitatem productam à superiori parte occipitii à posteriori ossis sincipitis et ossis petrosi."

This looks like the origin of the division into three lobes, while Willis seems to have originated the division into two.

"Porro in homine cui cerebrum præ ceteris animalibus capax et amplum est, utrumque hæmisphærium rursus in duos lobos nempe anteriorem et posteriorem subdividitur: inter quos arteriæ carotidis ramus, utrinque instar rivi limitanei productus eos veluti in binas provincias distinguit."—Willis, Cerebri Anatomè, 1664.

[2] Leçons d'Anatomie Comparée, 2de ed., tome iii., p. 44.

medius; *c*, lobus posterior, "*cerebellum obtegens.*" Fig. 2, represents the brain of "*Simia rhesus;*" and the explanation of the figures says: "*a*, lobus anterior; *b*, lobus medius; *c*, lobus posterior." Fig. 3, a figure of the brain of *Simia sabœa*, and fig. 4, of "*Simia capucina*," have the same lettering, and the letters have the same signification.

And, to permit of no mistake, Tiedemann, at page 48 of the same work, tells us expressly :—

"Cerebrum simiarum quoad magnitudinem et divisionem in lobos ad humanum proxime accedit: dividitur enim per fissuram mediam longitudinalem in duo æqualia hemisphœria *quorum utrumque rursus in tres lobos partitur. Lobi posteriores uti in homine faciem superiorem cerebelli obtegunt.* In cæteris a nobis dissectis quodrupedibus encephali hemisphæria sunt magis plana et brevia. Lobi posteriores quamvis breviores quam in Simiis tantommodo in Phoca occurrunt, in reliquis Feris in Leone, Fele, Nasua, Lotore, *et ipso Lemure* ac Bradypode cerebellum fere nudum vel ab hemisphæriis haud obtectum conspicitur."

In 1825, Tiedemann, describing the brain of the orang (Hirn des Orangs mit dem des Menschen verglichen), particularly states that each hemisphere is, as in man, divided into three lobes—an anterior, a middle, and a posterior; and that the ovate cerebral hemispheres cover the cerebellum almost entirely, though they do not, as in man, project beyond its posterior margin.

In the third volume of the second edition of the "Leçons," Cuvier expressly affirms, in speaking of the apes :—

"Their hemispheres are also prolonged backwards, as in man, to form the posterior lobes, which repose on the cerebellum.

"The cerebellum is almost wholly covered by the hemispheres in the seal and otter.

"In the dolphin, a large proportion of the cerebellum is covered."—pp. 84-86.

And, in the "Regne Animal," he gives as part of the definition of the order Quadrumana: "Le cerveau a trois lobes de chaque côté, dont le postérieur recouvre le cervelet."

In his elaborate essay "On the brain of the negro, compared with that of the European and the orang outang," published in the Philosophical Transactions for 1836, Tiedemann's zeal for the cause of the oppressed black has occasionally led him into something very like special pleading; and yet he does not dream of hinting the absence of the posterior, or third lobe, present in the

negro's brain, from that of the orang. His summary, at p. 518, runs thus :—

" The brain of the monkey and the orang outang differs, as follows, from the human brain :—

" 1. The brain is absolutely and relatively smaller and lighter, shorter, narrower, and lower than the human brain.

" 2. The brain is smaller, in comparison to the size of the nerves than in man.

" 3. The hemispheres of the brain are, relatively to the spinal marrow, medulla oblongata, the cerebellum, corpora quadrigemina, the thalami optici, and corpora striata, smaller than in man.

" 4. The gyri and sulci of the brain are not so numerous as in man."

I do not think that any valid objections can be raised as to the accuracy of the statements already cited; but in case such should be brought forward, I will now produce one authority which I am sure Professor Owen will regard as irrefragable. This is the third volume of the Catalogue of the Hunterian Collection, where, at p. 34, I find the following passages :—

" 1338. The brain of a baboon (*Papio mormon*, Cuv.) The cerebral hemispheres are of greater proportionate size than in any of the preceding specimens, and they are developed so far backwards as to cover the cerebellum. The posterior lobes exhibit anfractuosities characteristic of the brain in the higher simiæ, as the baboons and orangs.

" 1338A. The brain of a chimpanzee (*Simia troglodytes*, Linn.) This brain, in the relative proportions of the different parts, and the disposition of the convolutions, especially those of the posterior lobes, approaches nearest to the human brain. It differs chiefly in the flatness of the hemispheres, in the comparative shortness of the posterior, and the narrowness of the anterior lobes."

In the year 1842, Dr. Macartney read a paper " On the Minute Structure of the Brain of the Chimpanzee, and of the Human Idiot, compared with the perfect Brain of Man," before the Royal Irish Academy; and the essay, accompanied by two plates, is published in the 19th volume of the Transactions of that Academy. At p. 323, Dr. Macartney says—" The proportions of the cerebellum to the cerebrum were exactly as in man." " The parts in the lateral ventricles corresponded very nearly with the same in man." The figure of the upper surface of a plaster cast of the brain of this Chimpanzee, in Plate I., distinctly exhibits the posterior cerebral lobes projecting beyond the cerebellum.

The "Verhandelingen over de Natuurlijke Geschiedenis der Nederlandsche overseesche Bezittingen," pp. 39-44, contains a valuable memoir,[1] by Dr. Sandifort, on the anatomy of the orang, in which, at p. 30, I find the following distinct statement :—

"The base of the brain is divided into three lobes (lobi), of which the most anterior is short ; the middle one descends remarkably below the foremost and hindmost ; while the hindermost not only covers the cerebellum, but extends still further backwards than it. In vertical sections of the skulls of full-grown specimens, the bony framework showed that such is always the case, so the cerebral lobes appear to extend more backward over the cerebellum as age advances. In the brain investigated by Tiedemann, which belonged to a young orang, the cerebral lobes covered the cerebellum, but did not extend further back than it."

Vrolik, in the valuable article, "Quadrumana," contributed by him to "Todd's Cyclopædia" (1847), expressly affirms (p. 207), that, in the orang, the cerebral hemispheres "are protracted behind the cerebellum." And M. Isidore Geoffroy S. Hilaire ("Seconde Mémoire sur les Singes Americanes," Archives du Muséum, 1844) draws particular attention to the fact, that in the Saimiri, *Chrysothrix* (*Saimiris*, I. G. St. H.) *ustus*, a platyrhine monkey, and therefore far more distant from man than the tailless catarrhine apes of the old world, the cerebral hemispheres project far back beyond the cerebellum, though the latter is very well developed—in fact, as the cerebral hemispheres project nearly a centimetre behind the cerebellum, while the whole brain is only $5\frac{1}{2}$ centimetres long, the backward projection of the third lobe is, in this monkey, relatively greater than in man.

The "Transactions of the Royal Netherlands Institute at Amsterdam for 1849" contain one of the most valuable memoirs on the cerebral organization of the higher apes that has yet been written, entitled, "An Anatomical Investigation of the Brain of the Chimpanzee," by Schrœder van der Kolk and Vrolik. In their two plates they represent the brains of a chimpanzee, an orang, and a new-born child, and, in all, the letter *c* is applied to the same part—the posterior or third lobe, which they term "achterhoofds-kwab," "occipital lobe," in the explanation of the plates, or frequently in the text, "achter-kwab," "posterior lobe" ; nor among the heads of their careful enumeration of the differences between the brain of man and the higher apes does any one of the three differential characters whose existence I have denied find a place.

Finally, in the preface to the most elaborate special memoir that

[1] "Ontleedkundige Veschouwing van een Volwassen Orang oetan (*Simia satyrus*, Linn.), van het Mannelijk Geslacht."

has yet appeared upon the conformation of the brain in the higher Mammalia—the "Mémoire sur les plis Cérébraux de l'Homme et des Primatés," by M. P. Gratiolet,—I find the following passage (p. 2):—

"The convoluted brain of man and the smooth brain of the marmoset resemble one another in the fourfold character of a rudimentary olfactory lobe, *a posterior lobe, which completely covers the cerebellum*, a well-marked fissure of Sylvius, and lastly, *a posterior cornu to the lateral ventricle.* These characters are met with in combination only in man and in the apes."

M. Gratiolet's beautiful original figures of the brain of the chimpanzee (Pl. vi), and of the orang (Pl. vii), show quite clearly that the hinder margin of the cerebral lobes in these animals, when the brain is in its natural condition, overlaps the hinder margin of the cerebellum.

Many months ago, having learned that my friend Dr. Allen Thomson had at one time occupied himself with the dissection of the brain of the chimpanzee, I applied to him for information, and he has very kindly allowed me to print the following extracts from his letters. Of the first brain he examined—that of a young female chimpanzee, seven or eight months old,—this eminently careful anatomist and physiologist says (under date of May 24, 1860):—

"There is, very clearly, a posterior lobe, separated from the middle one by as deep a groove between the convolutions on the inner side of the hemispheres, as in man, and equally well marked off on the other side. I should be inclined to say, that the posterior lobe is little inferior to that of man, excepting, perhaps, in vertical depth. The cerebral hemispheres completely covered the cerebellum, as seen from above. I took pains to observe this while the brain was still within the cranium, looking down upon it at right angles to the longitudinal axis of the cranial cavity, and I found the posterior extremity of the cerebral hemispheres projected a little beyond the vertical line, passing the back of the cerebellum."

Thus, every original authority testifies that the presence of a third lobe in the cerebral hemisphere is not "peculiar to the genus Homo," but that the same structure is discoverable in all the true Simiæ among the Quadrumana, and is even observable in some lower Mammalia; and any one who chooses to take the trouble to dissect a monkey's brain, or even to examine a vertically bisected skull of any of the true Simiæ, may convince himself, on the still better authority of nature, not only that the third lobe exists, but that it extends to the posterior edge of, if not behind the cerebellum.

2. *The posterior cornu.*—In the "Icones," already referred to, Tiede-

mann not only described but figured the posterior cornu of the lateral ventricle in the *Simiæ* (Tab. 2°, Fig. 3ª), as "*e.* scrobiculus parvus loco cornu posterioris;" and when giving an account of the brain of the seal (Tab. 3ª), he says: "*e.* cornu descendens s. medium. Præterea cornu posterioris vestigium occurrit."

Tiedemann's statements are confirmed by every authoritative writer since his time. According to Cuvier [1] (Leçons, T. iii., p. 103), "the anterior or lateral ventricles possess a digital cavity [posterior cornu] only in man and the apes. This part exists in no other mammifer. Its presence depends on that of the posterior lobes. In the seals and dolphins alone, in which the posterior part of the hemisphere is considerable, the lateral ventricle, at the point where it descends into the temporal tuberosity, bends a little backwards, thus exhibiting a sort of vestige of the digital cavity of the human brain."

Vrolik (Art. Quadrumana, Todd's Cyclopædia), though he carefully enumerates the differences observable between the brains of the Quadrumana and that of man, does not think of asserting the absence of the posterior cornu. And lastly, Schrœder van der Kolk and Vrolik (op. cit., p. 271), though they particularly note that "the lateral ventricle is distinguished from that of man by the very defective proportions of the posterior cornu, wherein only a stripe is visible as an indication of the hippocampus minor;" yet the figure 4 in their second Plate shows that this posterior cornu is a perfectly distinct and unmistakable structure, quite as large as it often is in man. It is the more remarkable that Professor Owen should have overlooked the explicit statement and figure of these authors, as it is quite obvious, on comparison of the figures, that his wood-cut of the brain of a Chimpanzee (l. c., p. 19), is a reduced copy of the second figure of Messrs. Schrœder van der Kolk and Vrolik's first Plate.

As M. Gratiolet (l. c., p. 18), however, is careful to remark, "unfortunately the brain which they have taken as a model was greatly altered (profondément affraissé), whence the general form of the brain is given in these plates in a manner which is altogether incorrect." Indeed, it is perfectly obvious, from a comparison of a section of the skull of the Chimpanzee with these figures, that such is the case; and it is greatly to be regretted that so inadequate a figure should have been taken as a typical representation of the Chimpanzee's brain.

3. *The Hippocampus minor.*—But even supposing that the posterior cornu of the lateral ventricle and its appendage, the hippocampus minor, were absent in the apes, and "peculiar to the genus Homo," what classificatory value would the distinction possess? This, of course,

[1] Leuret, Longet, and Stannius, agree with or, perhaps, only repeat Cuvier.

depends upon the constancy of the supposed distinctive character; but it so happens that, as every anatomist knows, the posterior cornu and the hippocampus minor, are precisely those structures which are most variable in the human brain. This is by no means a novel discovery. The work of the brothers Wenzel[1] has now been published nearly half a century, and it contains (pp. 144-146) the following account of the special researches of these observers on the posterior cornu and the hippocampus, which they call simply "Tuber":—

"*Tuber in cornu posteriore ventriculorum lateralium*:—Non semper plerumque tamen adest, et quidem utroque in latere sive in utroque cornu. Inter quinquaginta et unum, eo specialiter fine a nobis examinata cerebra diversæ omnino ætatis atque utriusque sexus, tria tantum reperiebamus in quibus tuber illud in utroque latere et duo in quibus uno in latere desiderabatur. Quam constans autem, in universum tuberis istius præsentia, tam varians est magnitudo illius, non in diversis tantum subjectis, sed etiam in uno eodemque absque omni prorsus et ætatis et sexus discrimine. Quandoque admodum longum, interdum latum nonnunquam valde angustum est. Magnitudo illius in universum spectata, sequitur magnitudinem posterioris cornu ventriculorum lateralium: hæc quam maxime diversa est, quin et in uno eodemque cerebro et utroque latere. Quandoque enim cornu istud fere usque ad posteriorem cerebri marginem pertingit, sæpe terminus prope initium est, sæpe contingit ut in minore cornu magis, in majore minus sit tuber, id quoque eodem nonnunquam in cerebro evidentissime animadvertitur. Rarius in hoc tubere est quod sicut hippocampus ad finem suum crenas sive sulcos habeat quod superficies ejus duo in tubera superius atque inferius, divisa sit; plerumque autem in medio latissimum est et crassissimum, in terminis angustius: sed et hoc quoque varium est.

"Situs illius atque interior structura semper sunt eadem. Semper juxta interius latus cornu videtur, ideoque superficiei cerebri prope adjacet, idque cum interiore ejusdem structura cohæret, quae, ut sectio in transversum ducta clare demonstrat, eadem omnino est ac in gyris cerebri. Constat videlicet ex interiore in laterales ventriculos continuato, sive prolongato pariete cujus gyri in superficie cerebri siti, qui inflectitur, ac deinde interiori de parte exteriorem versus ad superficiem cerebri rediens in alium gyrum transit. Paries ist intra cornu medullosa, quæ cornu ipsum vestit, lamina obducitur; paries ipse autem ex cinerea, in ambitu cerebri sita, ubique conspicua sub-

[1] Jos. et Car. Wenzel, "De penitiori structura Cerebri Hominis et Brutorum." Tubingæ, MDCCCXII.

stantia constat, quæ hoc loco neque latior est, neque alium colorem exhibet ac in quovis alio cerebri gyro.

"Inter utrumque tuberis parietem spatium invenitur, quod vasculosa cerebri æque explet ac sulcum inter duos alios gyras in superficie cerebri sitas.

"Si in superficie cerebri eo, qui eminentiæ isti opponitur loco membrana cerebri media et interior detrahitur, tuber illud evanescit, ut quamprimum cerebri superficies extenditur, in planum mutatur.

"Discrimen ergo, hoc tuber inter et processum cerebri lateralem in eo consistit, quod illud verum absolutum, gyris in exteriore cerebri superficie sitis omino simile, quoad interiorem vero structuram plane æquale, in interiore cerebro sive in aliqua ventriculorum ejusdam parte existens gyrus sit; quod e contrario hippocampus, si cum gyris in superficie cerebri existentibus comparatur, tantummodo gyri alicujus pars, non autem absolutus atque integer gyrus sit, cujus initium in interiore cerebro, aut in aliqua ventriculorum parte existit."

The brothers Wenzel figure in their excellent plates the various conditions of the posterior cornu and hippocampus minor to which they refer; and it is remarkable that the brain which they have selected as exemplifying the absence of the hippocampus minor on both sides, Tab. v., Fig. 1, is said to be "ex triginta annorum æthiope," while the most remarkably developed hippocampus, Tab. vii., Fig. 3, is "ex septem annorum puero."

The work whence these extracts are taken is contained in the libraries both of the College of Surgeons and of the Royal Society; but, even if it were inaccessible, a well-known and more modern writer fully bears out the doctrine it contains. I refer to Longet,[1] who states that, in the human brain, "the posterior cornu is found of very different lengths and breadths. I have found brains in which it extended up to within a few millimetres of the surface of the posterior lobe, and others in which it ended at more than three centimetres therefrom."

The same excellent authority, in describing the posterior cornu of the lateral ventricle, says:—

"Its inner and lower wall is raised by a convolution which forms a more or less distinct, and at times, double projection into the cavity itself. This projection (Hippocampus minor, eminentia unciformis, calliculus, unguis, calcar avis) was well described by Morand, and after him was called the 'Spur of Morand'—'Ergot de Morand.'

"The Hippocampus minor exhibits differences in its form and

[1] German edition, by Hein, under the title, Anatomie und Physiologie des Nervensystems des Menschen und der Wirbelthiere, 1847, Bd. i., p. 463.

circumference, as Greding has stated; usually it is bent on itself, arched forwards and outwards, sometimes narrow and long, sometimes broader. Very frequently it is smooth, at other times it exhibits many fissures and small enlargements, especially posteriorly; or it may be divided by a longitudinal cleft into two halves, the upper of which is almost always larger than the lower. Its dimensions are by no means directly proportional to the development of the posterior lobe. In the same subject it may be very distinct upon the one side, and yet be hardly perceptible upon the other. For the rest I can certify that, in spite of Meckel's[1] assertion to the contrary, it is not always present. My own observations agree with those of Wenzel, who, among fifty-one subjects that he examined with express reference to this point, found three in which the hippocampus was absent upon both sides and two in which every trace of it was absent upon one side only."

To allow a structural character totally absent in six per cent. of the members of any group to stand as part of the definition of that group, *considered as a sub-class*, would be a very hazardous proceeding. But, is it true that the hippocampus minor is altogether absent in the highest apes? I suspect that Tiedemann is responsible for the not unfrequently admitted doctrine that it is; for, in the "Icones" he writes:—

"Pedes hippocampi minores vel ungues, vel calcaria avis, quæ a posteriore corporis callosi margine tanquam processus duo medullares proficiscuntur, inque fundo cornu posterioris plicas graciles et retroflexas formant, in cerebro simiarum desunt; nec in cerebro aliorum a me examinatorum mammalium occurrunt. *Homini ergo proprii sunt.*"

However, the citation from the Memoir of Schrœder van der Kolk and Vrolik, given above, proves that in their opinion a rudimentary hippocampus minor does exist in the Chimpanzee, and Dr. Allen Thomson adds his valuable testimony in a still more decided manner to the same effect. In the letter which I have already quoted, he says:—

"I found an eminence in the floor of the posterior cornu and towards its inner side, which I regarded as the hippocampus minor, and I found it produced exactly in the same manner as in man, by the bulging into the ventricles of a portion of the brain, by a very deep groove between the convolutions."

In another letter (the 11th of November, 1860), replying to further troublesome inquiries of mine, Dr. Thomson writes:—

"I thought it best for my own satisfaction and yours, to open the

[1] Dr. Hein here adds: "What Meckel says is that he himself never failed to find the hippocampus minor, but that he by no means wishes to throw doubts on Wenzel's statements;" and on reference to Meckel's work, I find this to be quite correct.

lateral ventricle from above, in a second brain which I possess. This brain, which was extracted from a young animal in Africa, was placed in rum there, and it was both much discoloured and not so well preserved as I could have wished. The appearances are, however, sufficiently distinct to enable me to confirm entirely what I think I stated to you before, viz.: 1. The prolongation of the cavity of the posterior cornu, to a considerable distance beyond the plane of the posterior edge of the corpus callosum (which, I presume, may be taken as the best measure of the position of the parts); and 2. The existence on the inner side, and partly in the floor of that posterior cornu, of an eminence corresponding in all respects with the hippocampus minor. . . . Just as I was setting about the examination of this point, I found an opportunity, in my dissecting-room, of looking at a fresh human brain, and I thought it might be more satisfactory to examine the two brains together. It so turned out, that the brain I cut in upon presented an example (not uncommon) of great deficiency in the extent of the posterior cornu. I think it is worth sending you a sketch of it, for it is really scarcely more developed than that of the chimpanzee in this respect."

Having now, as I trust, redeemed my pledge to prove that neither the third lobe of the cerebrum, nor the posterior cornu of the lateral ventricle, nor the hippocampus minor, are structures distinctive of and "peculiar to the genus *Homo*," I may leave it to the reader to decide the fate of the "sub-class *Archencephala*," founded upon the supposed existence of these three distinctive characters.

And here I might fairly leave the question; but essential as I have felt it to be to my personal and scientific character to prove that my public assertions are entirely borne out by facts, I am far from desiring to deal with this important matter in a merely controversial spirit. Therefore, although the differences hitherto referred to are certainly non-existent, I proceed to inquire whether there are any other marked and constant characters by which the human may be distinguished from the Simian brain.

Without doubt such characters are to be found; and in all probability, as in the case of any other two distinct genera, the more carefully and minutely our inquiries are carried out, the greater will be the number of these differentiæ. So far as my knowledge goes, the most prominent and important are the following:—

1. In the anthropoid apes the brain is smaller, as compared with the nerves which proceed from it, than in man.

2. In the anthropoid apes the cerebrum is smaller, relatively to the cerebellum, than in man.

3. In the anthropoid apes the sulci and gyri are generally less com-

plex, and those of the two cerebral hemispheres are more symmetrical, than in man.

4. The hemispheres are more rounded and deeper in man than in the anthropoid apes, and the proportions of the lobes to one another are different. Furthermore, certain minor gyri and fissures, present in the one, are absent or rudimentary in the other.

The evidence of the first of these differences has, I believe, been universally admitted since the time of Sœmmering. The second and fourth clearly result from the observations of Schrœder van der Kolk and Vrolik, and those of Gratiolet (Mém. sur les plis cerebraux des Primatés, 1854), as will appear from the following extracts. The first citation is taken from the work of the first-named authors, which seems to be so little known in this country, that I make no apology for length of the extract:—

"According to very precise investigations which the first-named of us has carried out with reference to this point, the difference between the brains of the higher apes and that of man is to be sought, not only in the smaller size of the hemispheres, but also in a totally different relation of the lobes. Relatively, the under surface of the first lobe of the cerebrum, in the chimpanzee, is much larger than in man; while, on the other hand, the distance from the most anterior point of the middle lobe to the hindermost point of the posterior lobe is much smaller. In our chimpanzee the distance from the root of the olfactory nerve to the anterior margin of the brain is about 44 millimetres, from the point of the middle lobe to the extreme end of the posterior lobe, 69 mm. In the adult man, according to measurements which the first of us has instituted, and which wholly agree with those of the ninth plate of Foville, the first named measurement is 57 mm., the second, 145 mm. In the brain of a new-born child, examined by us, the first dimension amounted to 33 mm., the second to 70 mm. The length of the base of the anterior lobe was thus to the distance from the point of the middle lobe to the end of the posterior lobe, in the chimpanzee, as 1 : 1·52; in the adult man as 1 : 2·54; in the child, as 1 : 2. Hence it appears that the relative proportions of the lobes of the child's brain hold just the mean between the chimpanzee and the adult man; and that in the course of the growth of the child to manhood, the posterior and middle lobes increase more in length than the base of the anterior lobe. In the orang, the same proportion obtains as in the new-born child, or 1 : 2, a result which is certainly remarkable, and proves that, in this respect, the brain of the orang stands higher than that of the chimpanzee. The second point to which we would direct attention is, that in comparing the brain of man with that of animals, and especially

in determining in what manner the cerebellum becomes covered, we too exclusively attend to the posterior elongation of the cerebral hemispheres, while the varying size of the cerebellum itself ought to be taken into account. On comparing the perpendicular section of the brain of the new-born child (pl. ii., fig. 3.) with fig. 1, the brain of the three-year-old chimpanzee, and with fig. 2, that of the orang of a like age, it is at once apparent that the cerebellum of the orang, and especially of the chimpanzee, is much larger than that of the child ; so that, supposing one could place the cerebellum of the chimpanzee behind the medulla oblongata of the child, it would be even less covered.

"In fact, the distance from the anterior edge of the most anterior part of the cerebellum, close to the corpora quadrigemina, to its posterior margin, measures, in the chimpanzee, 38 mm. ; in the orang, 35 mm. ; in the child, 22 mm. If we compare the measurements with the whole distance from the anterior to the posterior lobe of the cerebrum, we obtain, according to measurements taken by the first named of us,—

Chimpanzee, ...	38 : 101 mm.	= 1 : 2·66.
Orang, ...	35 : 96	= 1 : 2·74.
Human child, ...	22 : 96	= 1 : 4·36.
Adult man, ...	50 : 157	= 1 : 3·1.

"Hence, it is clear 1°, that the cerebellum in the Chimpanzee and in the Orang are proportionally larger than in man ; 2°, that the Orang in this respect approaches man more closely than does the Chimpanzee."—"Anatomical Investigation," &c., l. c. pp. 265-7.

The authors go on to remark that the same large proportion of the cerebellum to the cerebrum is characteristic of the lower Mammalia, as Sœmmering had already observed, and that, consequently, the uncoveredness of the cerebellum arises as much from the disproportionately large size of the latter, as from the defect of the posterior lobe of the cerebrum. They further show that the human cerebellum is proportionally still smaller in a six-months' fœtus (1 : 4·7); and that, while in the adult the cerebellum has more than double the size it had in the new-born child (50 : 22), the cerebrum of the adult is only $1\frac{1}{2}$ times as large in the adult as in the new-born child (157 : 96). At the same time the cerebellum attains its full size by the end of the third year—a fact which indicates very interestingly the relations of the cerebellum with the locomotive power.

M. Gratiolet commences his description of the cerebral convolutions of man thus :—

"The form of the human brain is well known. Its singular height,

the width of the frontal lobe, whose anterior extremity, instead of narrowing to an acute point, is terminated by a surface whose extent corresponds to that of the frontal bone; the large angle which the two orbital fossæ form, the depression of the fissure of Sylvius, the richness and complications of the secondary convolutions, at once distinguish this brain from that of all the Primates. But these differences, great and characteristic as they may be, yet consist with the existence of such analogies between the brain of man and that of apes, that the same general description serves both equally well. There are the same principal divisions, the same lobes, the same convolutions; all the parts are not the same, but they are homologous."—L. c., pp. 57, 58.

M. Gratiolet then goes on to point out what the differences of these homologous parts are; but I cannot give them in detail here, without entering upon a full explanation of his terminology, which would occupy too much space.

There is no lack, then, of real differences enough between the brain of man and those of the highest Quadrumana, though they are not those which have been asserted to exist. The question, what is the value of these differences? could only be satisfactorily answered, if the extent of variation exhibited by the brain among the different races of mankind had been carefully determined. We are greatly in want of knowledge on this important subject; but what little is known tends distinctly to the conviction, that no very great value can be set upon these distinctions, inasmuch as the differences between the brains of the highest races and those of the lowest, though less in degree, are of the same order as those which separate the human from the simian brain. I am well aware that it is the fashion to say that the brains of all races of mankind are alike; but in this, as in other cases, fashion is not quite at one with fact.

Sœmmering and Tiedemann are directly at variance with respect to the relative proportions of the size of the nerves to the brain in the higher and in the lower races of mankind; and, as respects the relative proportions of the cerebrum and cerebellum, the ratios deducible from Tiedemann's measurements give so small a difference, that though it is rather in favour of the existence of a larger proportional size of the cerebellum in the lower races, I do not think it can be depended upon.

But, with regard to the third especially Simian cerebral character mentioned above, Tiedemann's observations (though, as the negro's advocate, he endeavours to explain them away) are definite, and to the point:—

"The only similarity between the brain of the negro and that of the orang outang is, that the gyri and sulci on both hemispheres are

more symmetrical than in the brain of the European. It remains, however, to be proved whether this symmetry is to be found in all negro brains, which I very much doubt."—L. c., p. 519.

One would like to know the ground of Professor Tiedemann's doubts, because the only other observation he details, bearing on this subject, leads him to precisely the same conclusion. Thus, at p. 316 of the same memoir, I find the express statement:—"This [symmetry] is particularly visible in the brain of the Bosjes woman." Indeed, the fact must at once strike every one conversant with the ordinary appearance of a European brain, who glances at Pl. XXXIV. of Tiedemann's Memoir, in which a view of the Bosjesman brain referred to is given.

Fortunately, M. Gratiolet has also particularly described and carefully figured this brain (which is that of the "Hottentot Venus;" who died in Paris, and had the honour of being anatomized by Cuvier), and his remarks upon the subject are exceedingly important and instructive:—

"This woman, be it premised, was no idiot. Nevertheless, it may be observed, that the convolutions of her brain are relatively very little complicated. But what strikes one, at once, is the simplicity, the regular arrangement of the two convolutions which compose the superior stage of the frontal lobe. These folds, if those of the two hemispheres be compared, present, as we have already pointed out, an almost perfect symmetry, such as is never exhibited by normal brains of the Caucasian race. . . . . This regularity—this symmetry, involuntarily recall the regularity and symmetry of the cerebral convolutions in the lower species of animals. There is, in this respect, between the brain of a white man and that of this Bosjesman woman a difference such that it cannot be mistaken; and if it be constant, as there is every reason to suppose it is, it constitutes one of the most interesting facts which have yet been noted."—L. c., p. 65.

"The antero-superior curve is less convex than in the white man: lastly, the orbital fossæ are more concave; and there may be observed at the level of the anterior extremity of the temporo-sphenoidal lobe, a very marked constriction, which results from a very remarkable predominance of the supraciliary lobe. This disposition appears to result from the less development of the superior divisions. The brains of fœtuses belonging to the white race present it at the maximum, when the operculum of the fissure of Sylvius does not yet cover the central lobe; it is still quite apparent at birth; but it becomes slowly effaced with age, and in the adult it has completely disappeared. The brain of the Hottentot Venus is, then, in all respects, inferior to that of white men arrived at the normal term of their development. It can be

compared only with the brain of a white who is idiotic from an arrest of cerebral development."—p. 66.

Finally, with respect to the fourth difference, Tiedemann observes (p. 515) of the negro's brain:—

"The anterior part of the hemispheres is something narrower than is usually the case in Europeans. This is particularly remarkable in the brain of the Bosjes woman."

Thus, the cerebral hemispheres of the Bosjesman (and to a certain extent of the negro), so far as the evidence before us goes, are different from those of the white man; and the circumstances in which they differ—viz., the more pointed shape of the cerebral hemispheres, the greater symmetry of their convolutions, and the different development of certain of these convolutions,—are all of the same nature as most of those which distinguish the ape's brain from that of man. In other words, if we place A, the European brain, B, the Bosjesman brain, and C, the orang brain, in a series, the differences between A and B, so far as they have been ascertained, are of the same nature as the chief of those between B and C.

The brains of the lowest races of mankind have been hardly at all examined; and it would be a matter of great interest to ascertain whether, in these races, there is any trace of the external perpendicular fissure, any diminution of the lobule of the marginal convolution, and any increase of the proportional size of the nerves to the cerebral mass. Medical men living at the Cape of Good Hope, in Australia, and within reach of the Hill-men of India, will, it is to be hoped, some day solve these problems for the zoologist.

Let it be admitted, however, that the brain of man is absolutely distinguished from that of the highest known apes—

1st. By its large size, as compared with the cerebral nerves;

2nd. By the existence of the lobule of the marginal convolution;[1]

3rd. By the absence of the external perpendicular fissure—

And then let us turn to the other side of the argument, and weigh these differences against those which separate the brains of *Pithecus* or *Troglodytes* from those of the lowest Quadrumana.

The brain of *Lemur mongos* is well figured, and constantly referred to by Tiedemann in the "Icones" so often referred to. The few gyri; the shortness of the cerebral hemispheres, in the region of the third lobe, which leave fully half the cerebellum uncovered; the large size of the vermis superior; the prominence of its flocculus; the great size of the olfactory nerves, which rather deserve the name of olfactory

[1] The second and third differences are mentioned by Gratiolet, to whose Memoir I must refer for a statement of their nature.

lobes; the singleness of the corpora candicantia; the comparatively small and flat pons varolii; the presence of corpora trapezoidea; and, in the internal structure of the brain, the large size of the optic thalami in relation to the corpora striata, and the total absence of a posterior cornu to the lateral ventricle[1]—are all characters which are perfectly obvious, and which separate the brain of the *Lemur* as completely from that of *Pithecus* or *Troglodytes*, as from that of man.

The description of the brain of *Stenops tardigradus*, by Vrolik, tells the same story even more strikingly; and the brains of *Perodicticus* and other Prosimiæ, exhibited in the Hunterian Museum, fully bear out the conclusion, that the vast differences noted obtain throughout the Prosimian division of the Quadrumana.

M. Gratiolet, in fact, has been so struck by the immense discrepancy between the Simiæ and Prosimiæ in cerebral structure, that he proposes to consider the latter as forming a part of the order Insectivora. In this view he is at variance with all the other zoologists; but, in order to meet all possible objections, I will, for the moment, suppose that he is right, and that the order Quadrumana should be restricted to the Simiæ. Even on this supposition, the force of my argument remains unchanged; for the brains of the lower true apes and monkeys differ far more widely from the brain of the orang than the brain of the orang differs from that of man. Not only do they differ from the orang (and to a greater degree) in most of those respects in which the orang differs from man, but they present the absolute distinction, that while the orang, like man, has two corpora candicantia, the lower apes, like the other Mammalia, have only one.

In respect of their cerebral characters, therefore, I hold it to be demonstrable that the Quadrumana differ less from man than they do from one another; and that, hence, the separation of *Homo* and *Pithecus* in distinct sub-classes, while *Pithecus* and *Cynocephalus* are retained in one order, is utterly inconsistent with the principle of any classification of the Mammalia by cerebral characters.

On a future occasion I propose to take up the question, whether, on other grounds, there is any reason for departing from the Linnean view, that man is to be regarded as a genus of the same order as that which contains the Quadrumana.

[1] "Cornu posterius in Simiis et Phocis brevissimum et vix conspicuum est: in cæteris mammalibus plane desideratur."—Icones, p. 54.

XXVII

ON THE BRAIN OF ATELES PANISCUS

Proceedings of the Zoological Society of London, 1861, *pp.* 247–260. (*Read June* 11*th*, 1861.)

PLATE XXIX. [PLATE 36].

THE brain of a Spider Monkey (*Ateles belzebuth*) has already been partially described and figured by M. Gratiolet in his remarkable memoir 'Sur les Plis Cérébraux des *Primatès*' (1854); but this careful observer had only old spirit specimens at his disposal, and it did not enter into his plan to give any account, either of the internal structure of the cerebrum, or of its relations to the cerebellum, or of the cerebellum itself. Hence a new description, which should touch upon these points, could hardly be superfluous, under any circumstances; while, at the present moment, the controversy which has arisen respecting the nature and the extent of the differences in cerebral structure between Man and the Apes gives an especial value to all new facts.

It has been affirmed—and a proposed new classification of the Mammalia has been largely based upon the assertion—that the brain of Man is distinguished from that of all Apes by possessing a posterior lobe, a posterior cornu to the lateral ventricle, and a hippocampus minor—these structures being absent in all Apes, even the highest.[1]

I have elsewhere[2] exposed the fallacy of these distinctions as applied to the Apes in general; Dr. A. T. Thomson[3] and Dr. Rolleston[4]

[1] Prof. Owen "On the Classification, &c., of the Class Mammalia," Proc. of Linnean Society, 1857; Reade's Lecture, 1859; Athenæum, March 23, 1861.

[2] Natural History Review, No. 1, January, 1861; Athenæum, April 13th, 1861.

[3] Nat. Hist. Review, No. 1, January, 1861.

[4] Nat. Hist. Review, No 2, 1861.

have proved the existence of the three structures referred to in the Chimpanzee and the Orang, by investigations upon the brains of these animals, undertaken with especial reference to the questions under discussion; and I propose to continue the process of rectification thus commenced, by inquiring into another special case—that of *Ateles paniscus*—and proving, by direct demonstration of the facts, that the three structures, said to be absent even in the highest Apes, are, on the contrary, largely developed[1] in this comparatively low American monkey, possessed of but a rudimental thumb upon its hand, and provided with four more teeth than the Old World Apes and Man.

In fact, so far from its being true that the differences between Man and the Apes lie mainly in the cerebral characters, so often referred to, all the evidence now accumulated tends towards the belief that the only three, very striking, cerebral characters, absent in other Mammalia, which can be truly affirmed to be common to Man and the Old and New World *Simiæ*, are exactly these three,—the whole of the true Apes, so far as our present knowledge goes, possessing a posterior lobe, a posterior cornu to the lateral ventricle, and a hippocampus minor in that posterior cornu; while these structures, so far from being in a rudimentary condition, are often more largely developed, in proportion to other parts of the brain, in the Apes than in Man.

The figures 1 and 2 of Plate XXIX. [Plate 36] represent the brains of a male and of a female *Ateles* of about the same size, as seen from above: both figures were drawn under my own eye by a very competent artist, and are in all essential respects perfectly faithful. It is nevertheless obvious that they differ greatly—so much, in fact, that they might readily be supposed to have belonged to different species. The whole difference, however, is due to the circumstance that, while fig. 1 was drawn from an almost fresh brain, fig. 2 represents a brain which has been for several months in spirit.[2] The roundness of outline of the latter as compared with the former,

[1] Since this paper was read, Mr. Marshall, F.R.S., has published, in the third number of the 'Natural History Review' (July 1861) a valuable essay on the Chimpanzee's brain, illustrated by photographs of the parts said to be absent; and Mr. Flower, in a paper read before the Royal Society (June 20th, 1861), has demonstrated over again the presence of the same parts in the Orang's brain, has shown their large development in *Cebus*, and has even proved the presence of a large posterior cornu and of a hippocampus minor in the Lemurine *Otolicnus*!

[2] The brain of *Ateles belzebuth*, figured by M. Gratiolet, pl. 10, figs. 1, 2, 3, 4, has undergone the same alteration as that represented in my fig. 2, as might be expected from the fact of its having been long preserved in spirit.

and the more transverse direction of the fissure of Rolando, are very remarkable; for the skulls of the two specimens show no particular difference of form. In the unaltered brain, figs. 1, 3, 4, the narrowness of the frontal lobes anteriorly, the excavation of their orbital faces, and the flatness of the superior contour are especially worthy of notice. Viewed from above, no part whatsoever of the cerebellum is visible, either at the sides or behind; while a profile view shows that the cerebral hemispheres projected, for at least $\frac{1}{10}$th of an inch, behind the posterior edge of the cerebellum. Whether this represents the total amount of cerebral overlap or not, I cannot say, in the absence of a vertical section of an *Ateles*' skull; but it is amply sufficient to prove that, even accepting as the definition of the posterior lobe the novel formula "All that part of the hemisphere which covers the posterior third of the cerebellum and passes behind it," *Ateles* is provided with a well-developed posterior lobe.

In this respect, as I have already said, it resembles all the Old and New World *Simiæ* which have yet been examined,—the only genus, within my knowledge, which even comes near to presenting an exception being *Mycetes*. I have not, indeed, had the opportunity of dissecting the brain of this monkey (nor has M. Gratiolet been enabled to give any account of it); but the Curator of the Hunterian Museum having kindly permitted me to have a vertical longitudinal section of the skull of a *Mycetes* made, I found not only that the plane of the tentorium (and consequently the inferior margin of the posterior lobes of the cerebrum) had a much greater inclination than in any other Simian (making an angle of as much as 45° with the base of the skull), but that the cerebral overlap, measured in the manner described by me in the *Athenæum* for April 13th, 1861, does not exceed $\frac{1}{20}$th of an inch, though the maximum length of the cranial cavity is 2·4 inches. Notwithstanding this reduction of the posterior lobe, however, the contrast between *Mycetes*, as a true Simian, and a *Lemur* is very striking, especially if both be simultaneously compared with some lower Mammal, such as the Dog. The occipital foramen in *Mycetes* is situated altogether upon the posterior face of the skull, and the condyles look completely backwards, as in the Dog; while the occipital crest is placed as near the postero-superior margin of the skull as in that animal. In both, the posterior face of the skull looks backwards, and not appreciably downwards. But in the Monkey the inclination of the tentorium, large as it is, is far less than in the Dog. The inner face of the occipital bone beneath the tentorium is not excavated, and the cerebral lobes projected beyond the cerebellum when the palate was horizontal. In

the Dog, on the contrary, the internal surface of the occipital bone below the tentorium is much excavated; and, when the palate was horizontal, the posterior edge of the cerebellum must have projected far beyond the cerebral lobes.

In *Lemur catta* the inclination of the tentorial plane is hardly greater than in *Mycetes*; but if the palatal line be made horizontal, it will be found that the posterior boundary of the cerebellar chamber projects for $\frac{1}{5}$th of an inch beyond that for the cerebrum, although the greatest length of the cranial cavity is only 1·9 inch. In fact, the cerebral hemispheres of the Lemur have a less backward development than those of the Dog. I believe that all the Lemurs are in the same case, and that the *Prosimiæ* are sharply defined from the *Simiæ* by the fact of always having more or less of their cerebellum uncovered; so that, by this character alone, the Lemurine brain is far more widely separated from that of any Simian, than the latter is from the human brain.

While one American Monkey (*Mycetes*) is, if the development of its posterior lobes only be taken into account, at the bottom of the series of *Simiæ*, if the same character alone be considered, another Simian, inhabiting the same geographical area, is at the top; I refer to *Chrysothrix sciureus*, whose posterior lobes, as I. G. St.-Hilaire long ago proved,[1] are better developed than those of any other Mammal, overlapping the cerebellum by one-fifth of their length. In fact, if the *Primates* were arranged according to the development of their posterior cerebral lobes we should have some such descending series as the following:—*Chrysothrix*, *Cebus*, *Troglodytes*, Man, ... *Mycetes*—a series which sufficiently illustrates the classificatory value of these structures. So much for the posterior lobe. I turn now to the next point, the demonstration of the existence of the posterior cornu in *Ateles*.

When the lateral ventricle was exposed in the ordinary way (Pl. XXIX. [Plate 36] fig. 5) a straight line passing from the extremity of the anterior to that of the posterior cornu measured 2·1 inches. A distance of 1·3 inch separated the anterior end of the anterior cornu from the commencement of the descending cornu; while a straight line extending from the commencement of the descending to the end of the posterior cornu measured 0·75. Each lateral ventricle, measured from the centre of the corpus callosum to the outer boundary, at its widest point, or opposite the commencement of the descending cornu, was about half an inch wide. The posterior cornu has a general direction backwards, outwards, and then

[1] See the 'Zoologie du Voyage de la Vénus' for an excellent figure of this brain.

inwards; and, besides its general curvature, it has a secondary inflexion, so as to be a little sinuous. It is wide at its commencement, but rapidly narrows, until, where it bends inwards, its walls are so close together as to give it the appearance of a mere fissure, whose sides are apt to adhere together in such a manner as seriously to interfere with the satisfactory definition of the posterior limits of the cornu. In preparing the specimen, of which fig. 5 is a representation, for the artist, I therefore took care not to extend these limits artificially, rather preferring to leave a portion of the cornu unopened than to exaggerate its length.

In the other brain I found the posterior cornu, on the right side (dissected in the ordinary manner), to be traceable, without the least difficulty, to within a very short distance of the posterior limit of the hemisphere; while in the left hemisphere, which I examined by making successive vertical sections from behind forwards, the posterior cornu ended at fully a quarter of an inch distance from the posterior extremity of the hemisphere. Such sections are of particular value; for they show the extent of the cornu without any disturbance of its natural dimensions; and a comparison of the woodcuts (fig. 1) A, B, C, &c., and A′, B′, C′, &c., which represent two series of sections of corresponding regions of the Human and the *Ateles*' brain, will at once show that the relative dimensions of the posterior cornu are greater in the Monkey than in Man. I may remark that, of the left hemispheres of three human brains which I have dissected for comparison with *Ateles*, that whose sections are represented in the figures had its posterior cornu far better developed than the other two, in one of which the cornu was a mere fissure, while in the other it was excessively short, not extending for more than half an inch behind the corpus callosum.

Thus, not only does the posterior cornu of the lateral ventricle exist in *Ateles*; not only has it that backward, outward, and then inward curvature which has been wrongfully asserted to be peculiar to the homologous cavity in the human brain; but it is, in proportion, wider than in the human brain, and it is longer than in many human brains.

The third point in my argument is the demonstration of the existence of the hippocampus minor. But such strange confusion has been lately introduced into anatomical science, partly by a misapplication of well-understood terminology, and partly, to all appearance, by a want of proper acquaintance with the structure and nomenclature of the human brain, that I must begin *ab initio*, by a description of the latter, so far as regards the hippocampi and their related structures.

The term "Hippocampus minor" was first used by Vicq d'Azyr in the following passage of his famous *Traité d'Anatomie et de Physiologie* (tome i. 1786), where, in the Explication des Planches du Cerveau, pl. 6, p. 9, I find:—"26. 46. 45. Saillie ou relief qui se continue en 26 avec l'origine de la corne d'Ammon, et qui en 45 se recourbe en dedans: c'est la partie que Morand a appellée l'ergot."[1]

The term "hippocampus minor" has been used in the sense here defined by Vicq d'Azyr by all succeeding anatomists, as the following extract from the celebrated work on Human Anatomy, "Soemmering, vom Baue des menschlichen Körpers," Bd. IV. (Hirn- und Nervenlehre, umgearbeitet von G. Valentin) pp. 195, 196, will show:—"Der Sporn, oder die Klaue, oder der Vogelsporn, oder die Vogelklaue, oder der kleine Fuss des Seepferdes, oder der Nagel, oder der Stiefel, oder die Falte, oder der Hahnensporn, oder die hintere, oder kleinere, Wulst, oder die fingerförmige Erhabenheit (*calcar s. unguis, s. calcar avis, s. hippocampus minor, s. pes hippocampi minor, s. eminentia minor, s. digitata, s. unciformis, s. ocrea, s. colliculus*), bildet eine nach aussen und vorn convex gebogene Erhabenheit der inneren Wand des hinteren Hornes des Seitenventrikels."

"The hippocampus minor forms an elevation, convex outwards and forwards, of the inner wall of the posterior cornu of the lateral ventricle."

There can, therefore, be no doubt as to what is meant by the term 'hippocampus minor.'

Another elevation of the wall of the ventricle is known to human anatomists as the 'Eminentia collateralis,' for an authoritative definition of which I will again quote Soemmering's Anatomy, "Die seitliche Erhabenheit oder die längliche Seitenerhabenheit oder die Nebenerhabenheit (*eminentia lateralis, s. collateralis, s. Meckelii*), bildet eine wulstige Hervorragung welche vor dem Eingange in das hintere und neben dem in das untere Horn des Seitenventrikels liegt, und nach aussen von dem Ammonshorne sich befindet. Uebrigens wird diese Benennung offenbar auf verschiedene, variabele, grossere oder unbedeutendere, Erhabenheiten, die neben dem Ammonshorne, in dem

[1] "Ce relief est, comme la corne d'Ammon, ou hypocampe, formé d'une lame blanche à sa surface, et, plus profondément, de substance grise: il occupe l'angle interne du prolongement postérieur des ventricles latéraux, comme l'hypocampe celui du prolongement inférieur des mêmes cavités; et il ne diffère de cette production qu'en ce qu'il se termine par une pointe mousse, tandisque l'autre s'élargit en s'éloignant de son origine. On peut donc le regarder comme un petit hypocampe, et le désigner sous le nom de hypocampus minor par opposition avec l'hypocampus major, qui est la corne d'Ammon. Cette nomenclature m'a paru plus convenable que celle d'unguis, de colliculus, &c."

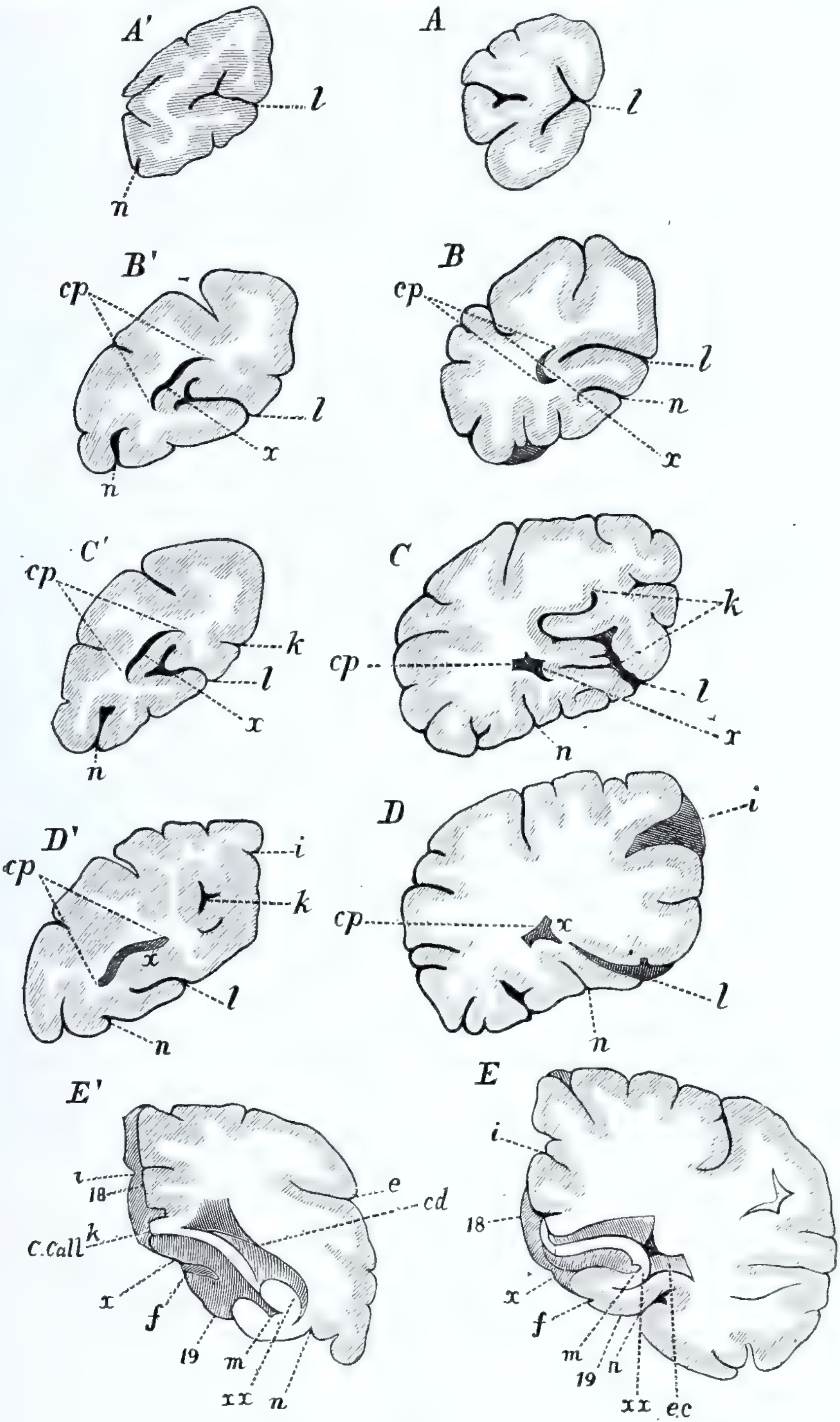


Fig. 1.—Transverse sections of corresponding (left) cerebral hemispheres of Man (A, B, C, D, E) and of *Ateles* (A′, B′, C′, D′, E′), taken perpendicularly to the plane of the corpus callosum, along the lines marked with corresponding letters in Fig. 2. *l.* calcarine sulcus; *n.* collateral sulcus; *i.* calloso-marginal; *k*, occipito-parietal sulcus; *c. p.* posterior cornu; *x.* hippocampus minor; *xx.* hippocampus major. A—D, A′—D′ viewed from behind; E and E′ from in front.

Bereiche des unteren Hornes des Seitenventrikels vorkommen, angewendet."

"The eminentia lateralis, or collateralis, or Meckelii, is formed by a rounded elevation which lies in front of the entrance into the posterior, and beside that into the inferior cornu of the lateral ventricle, and is situated external to the cornu Ammonis."

It will be observed that Valentin, who has taken great care to collect together the multitudinous synonyms of the parts of the brain, does not enumerate "pes hippocampi minoris" among those of the eminentia collateralis; nor has the term 'pes hippocampi minoris' been ever used in this sense by any anthropotomist of authority.

And if it be an error in terminology to apply the name of pes 'hippocampi minor*is*' to the eminentia collateralis, it is a still greater error, in point of anatomical fact, to assert that "the eminence continued backwards from the pes into the posterior cornu is the hippocampus minor."[1] If any eminence is continued backwards from the eminentia collateralis into the posterior cornu (as sometimes happens) it lies in the floor of the cornu, alongside the hippocampus minor, but perfectly distinct from it. But it will perhaps be better to demonstrate this elementary fact over again, though I feel that the doing so necessitates an apology to those who are conversant with the anatomy of the human brain.[2]

The lower figure of the woodcut (fig. 2) represents the inner surface of one of the hemispheres of the human brain. The contour is taken from one of Foville's Plates, but only the principal sulci are indicated,—those marked *l*, *m*, and *n* being put in from a specimen which I dissected, so as to ascertain their true nature. Of these sulci, that marked *i i* is the sulcus called by Gratiolet 'fronto-parietal,' a name which involves an ambiguity, and for which I therefore propose to substitute 'calloso-marginal,' as this sulcus lies between the corpus callosum and the margin of the hemisphere; *k* is the occipito-parietal sulcus (scissure perpendiculaire interne, *Gratiolet*); *l* is the posterior part of the "scissure des hippocampes" of Gratiolet. This sulcus is a very remarkable one. Commencing just in front of the posterior thickening of the corpus callosum, opposite *x*, it rapidly deepens as it

[1] Prof. Owen, Athenæum, March 23rd, 1861.

[2] Compare, for example, the well-known standard English 'Elements of Anatomy,' by Quain and Sharpey, where the relations of the eminentia collateralis and hippocampus minor to distinct convolutions are clearly pointed out (p. 710). Malacarne (Encefalotomia Nuova, 1780, part ii. p. 67) describes the continuation of the eminentia collateralis forwards into the descending cornu under the fanciful name of "Gamberuolo," or greave. It appears to be more constantly of large size than the continuation backward into the posterior cornu.

is traced backwards, and forms a great fissure, extending, in some parts, for as much as ¾ of an inch upwards and outwards, and passing backwards until it nearly reaches the posterior margin of the hemisphere, where it terminates by dividing into two short, but deep, branches, a superior and an inferior. Traced from before backwards, or from within outwards, the line of this sulcus presents a strongly marked, but irregular, upward convexity.

On making successive transverse sections of this cerebrum from before backwards (woodcut, fig. 1. A, B, C, D), the fissure was seen, in

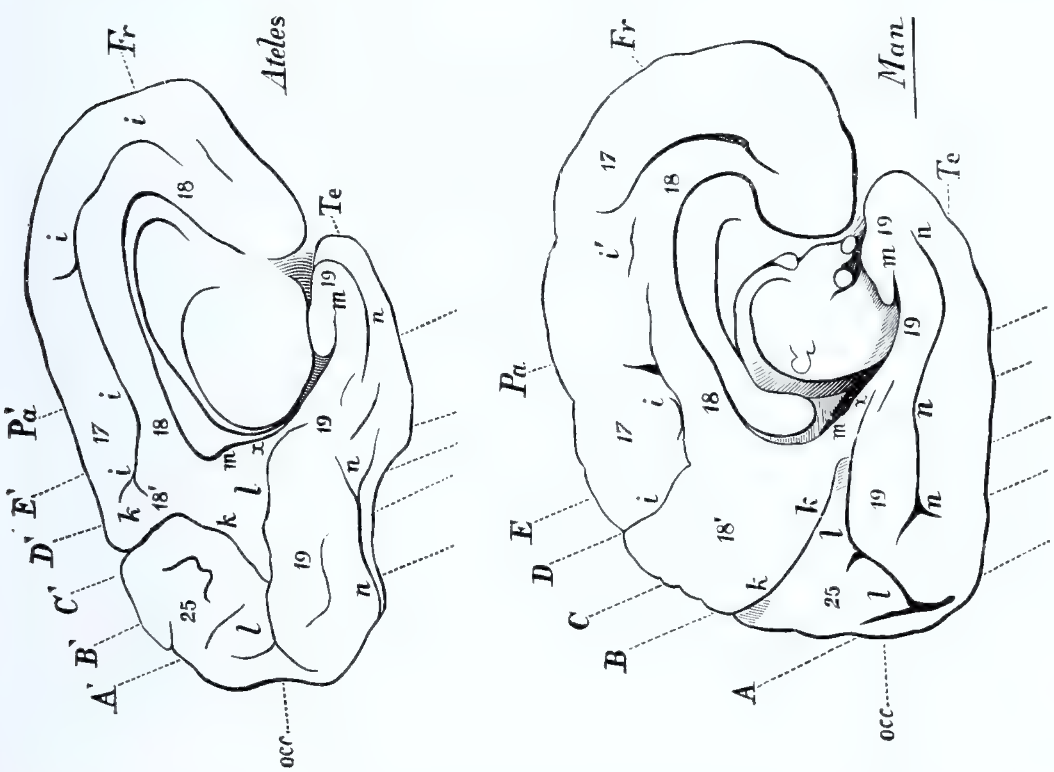


Fig. 2.—View of the inner surface of the left cerebral hemisphere of *Ateles*, of the natural size, and beneath it a corresponding view of the human left cerebral hemisphere reduced to the same size. In the latter only the principal sulci are indicated. *i.* calloso-marginal sulcus; *k.* occipito-parietal sulcus; *l.* calcarine sulcus; *m.* dentate sulcus; *n.* collateral sulcus; *x.* continuation of the callosal gyrus (18) into the uncinate gyrus (19). A, B, C, &c., A′, B′, C′, &c., the lines along which the transverse sections in Fig. 1 are taken.

its most posterior part (A), to pass almost horizontally outwards for a short distance, and then to divide into an upward and a downward branch. In front of A it forms a curve strongly convex upwards, without any terminal bifurcation; in B it is much longer and less convex; in C it is but slightly sinuous, and in D it is a little concave

upwards and inwards. Combining these views with those given in fig. 2, it is easy to form an estimate of the figure of the surfaces of the upper and under lips of the sulcus; but what is most important about it is, that, so far as the posterior cornu extends, the closed end of this sulcus corresponds with the hippocampus minor (x), which last is, in truth, nothing but the arch of cerebral substance which, at once, forms the outer boundary of the sulcus and the inner boundary of the cornu.

From its special relation to the hippocampus minor, or "calcar avis," I shall call this the "calcarine" sulcus; but it extends beyond the calcar and the posterior cornu, both anteriorly and posteriorly, particularly in the latter direction. Nevertheless it does, in a definite sense, correspond with the inner wall of the posterior cornu. The calcarine sulcus dies away anteriorly, at the point indicated, and is in no way continuous with that sulcus which has a relation to the hippocampus major similar to that of the calcarine sulcus to the hippocampus minor, and which, for distinction's sake, I will call the 'dentate' sulcus, on account of its relation to the fascia dentata or *corps godronné*. This narrow and well-known sulcus lies between the letters m and m, the lower m being placed opposite its termination in the fold formed by the recurved part (crochet de l'hippocampe, *Gratiolet*) of the so-called 'uncinate' convolution (19). Thus the dentate sulcus, which corresponds with the hippocampus major, is separated from the calcarine sulcus, which similarly answers to the hippocampus minor, by the rounded process of cerebral matter, x, this last being, in fact, the inferior and posterior continuation of the callosal gyrus (circonvolution de l'ourlet of Foville, pli du corps calleux of Gratiolet). This continuation of the callosal gyrus into the uncinate gyrus is regarded as an anomalous peculiarity of the human brain by M. Gratiolet (*l. c.* p. 64); but, so far as I have examined into the matter, it is similarly continued into the uncinate gyrus in Apes.

Ending at a point considerably anterior to the calcarine sulcus, sometimes in a bifurcated extremity, there is another deep sulcus, n, n, which runs, at first, roughly parallel with l, l, but is much longer, being continued along the inner and under surface of the temporal lobe nearly to its extremity. Although not so deep as the calcarine sulcus, it is continued upwards and outwards, for a considerable distance; and throughout its whole course, the bottom, or roof, of the sulcus underlies the floors of the descending and posterior cornua. If a vertical section be taken through the eminentia collateralis (E, p. 489), it will be found that the arch of cerebral substance, e c, whose

convex side receives that name, by its concave side bounds the sulcus in question: in other words, the eminentia collateralis stands in the same relation to *n n* as the hippocampus minor to *l l*, or the hippocampus major to *m m*. From the region especially named by anatomists "eminentia collateralis," the sulcus *n*, *n*, which may be conveniently termed the 'collateral' sulcus, is continued forwards and backwards, and preserves, as might be expected, a similar relation to the parts which are the continuation of the eminentia collateralis, viz. the floors of the descending and posterior cornua respectively, as it had to that eminence. It is difficult to imagine a much more definite proof, if any were wanted, that the hippocampus minor is in no sense a continuation of the eminentia collateralis.

In the brain whence the sections A to E were taken, the floors of both the descending and the posterior cornua were particularly broad (C, D); but even here the posterior cornu became a mere crescentic slit posteriorly (B). However, the continuation of the collateral sulcus was always directed upwards and outwards towards the bottom of the slit.[1]

A comparison of the views here given, of the inner face and of sections, of Man's brain, with, as nearly as possible, corresponding views of the brain of *Ateles* (woodcuts, figs. 1 and 2) is exceedingly instructive. The principal sulci alone exist in *Ateles*; so that its brain furnishes a sort of sketch map of Man's. The calloso-marginal sulcus, *i*, *i*, is easily recognisable; so is the occipito-parietal sulcus, *k*, *k*; though the latter, instead of being straight and forming an obtuse angle with the plane of the corpus callosum, as in Man, is strongly convex forwards,[2] and, on the whole, makes an acute angle with the same plane. As a consequence, the occipital lobe (*occ*) is much larger, proportionally, than in Man, while the quadrate lobule is *pari passu* smaller. The calcarine sulcus, *l*, *l*, has the same general direction and the same bifurcated termination, as in Man. Anteriorly, it ends just in front of the level of the posterior edge of the corpus callosum (the prominent uncinate gyrus must be pushed aside to see

[1] I have recently had the opportunity of dissecting ten human brains, and, in all, I have found the calcarine and collateral sulci to present the relations described above, with perfect constancy. On the other hand, nothing could be more variable than the length and form of the posterior cornu of the lateral ventricle, and the relative and absolute size of the hippocampus minor. In one of these brains—that of a negro—the posterior cornua were almost absent, not exceeding one-third of an inch in length on either side. In another the cornua were both 1¼ inch long and very wide, with a large hippocampus. Another had a posterior cornu ½ an inch long on the left side, 1 inch on the right. In yet another it was much longer on the right than on the left side, &c.

[2] I found this in both brains. M. Gratiolet represents the corresponding sulcus in *A. belzebuth* as nearly straight.

its termination, ; and it is, as in Man, separated from the dentate sulcus by the narrow prolongation of the callosal gyrus downwards into the temporal lobe, *x*. Lastly, the collateral sulcus, *n n n*, is traceable—though interrupted at intervals—through the same extent, as in Man; and of the three parts into which it is broken, the posterior is continued back even further than in him, and passes a little on to the outer and posterior face of the hemisphere. The greater proportional width of the uncinate gyrus, contained between the calcarine and dentate sulci above, and the collateral sulcus below, is marked in *Ateles*. The transverse sections (fig. 1. A′, B′, &c.) are no less strictly comparable to those yielded by the human brain, the chief differences being that, throughout the greater part of its length, the calcarine sulcus possesses the bifurcated outer extremity which its posterior part only presents in Man; and that the collateral sulcus is smaller and further out in proportion, and hence the uncinate gyrus is larger.

As to the hippocampus minor, the transverse sections (fig. 1) clearly show how much larger it is, proportionally, in *Ateles* than in Man; while the horizontal section (Pl. XXIX. [Plate 36] fig. 5) exhibits its exact correspondence with the definition quoted above—viz. "an elevation of the inner wall of the posterior cornu of the lateral ventricle, which is convex outwards and forwards;" and, as might be expected from the transverse section, it shows the larger proportional size and greater outward convexity of the Monkey's hippocampus minor.

The eminentia collateralis, on the other hand, is far less developed in *Ateles* than in the particular human brain whence the sections are taken; but it is quite distinctly visible at the junction of the posterior and descending cornua. The floors of both these cornua, however, are so narrow, that the eminentia can hardly be said to be continued into them, as it sometimes is into the posterior cornu, and almost always is into the descending cornu, in the human brain. Thus, in exact contradiction of what has been affirmed, it is the hippocampus minor which *is* developed, and the continuation of the eminentia collateralis backwards which is *not* developed in the Monkey.

The sulci and gyri of the outer surface of the cerebral hemispheres present in *Ateles paniscus* the same essential arrangement as in the *Ateles belzebuth*, described and figured by M. Gratiolet. Dividing the hemisphere into five lobes (frontal, parietal, median, temporal and occipital) the median (insula—Island of Reil) hidden between the lips of the Sylvian fissure, is a mere smooth convex projection, wider

above than below, or having somewhat the shape of a triangle, with its apex downwards and forwards, and wholly devoid of sulci. The small frontal lobe is divided by the horizontal sulci into the three infero-frontal, medio-frontal, and supero-frontal gyri. The antero-parietal sulcus is placed very far forward, at the commencement of the Sylvian fissure, joins the supero-frontal sulcus, and then sends a branch backwards. The postero-parietal sulcus (scissure de Rolando) is situated so far back that the antero-parietal gyrus (1[r] pli ascendant, Gratiolet) is exceedingly thick, and it passes backwards, as well as upwards, towards the inner and upper margin of the hemisphere, close to which it terminates. The postero-parietal gyrus (2[e] pli ascendant) widens superiorly, in consequence of the backward inclination of the upper part of the Sylvian fissure, to form the postero-parietal lobule (lobule du deuxième pli ascendant), which presents one or two minor sulci upon its surface, and has its inner edge notched by the upper end of the calloso-marginal sulcus. The temporal lobe, again, is plainly divided into the usual antero-temporal, medio-temporal, and postero-temporal gyri, and the occipital lobe has a horizontal sulcus which marks off an infer-occipital gyrus from an upper region representing the super- and medi-occipital gyri. In both brains I find a distinct occipito-temporal sulcus (scissure perpendiculaire externe), though M. Gratiolet states that this very Simian fissure is obliterated in *Ateles* (*l. c.* p. 76). However, he figures what I cannot but consider to be this sulcus in his pl. 10, f. 2.

Another point on which I am much inclined to differ from M. Gratiolet is that which he himself regards as a difficulty—viz. the extent of the fissure of Sylvius. I cannot find the "pli intermédiaire, très petit il est vrai," which he supposes (*l. c.* p. 75) to bound the upper extremity of the Sylvian fissure. On the contrary, it appears to me to be one continuous sulcus; and admitting this to be the case, it will not be longer than the Sylvian fissure of the Douroucouli (Gratiolet, pl. 11. figs. 10, 11). But if this be the fact then 6, fig. 4, will be the angular gyrus (pli courbe) and 14, fig. 4, will be the second annectent gyrus (deuxième pli de passage).

This interpretation, again, would diverge from that given by M. Gratiolet; but I must confess that, to me, the least satisfactory part of this able observer's treatise is that which relates to the identification of the angular gyrus and the annectent gyri, throughout the series of the *Primates*.

The transverse diameter of the cerebellum (Pl. XXIX. [Plate 36] figs. 4, 6, 7) is much larger, in proportion to its antero-posterior measurement, than in Man, and the sides of the upper surface slope

more away from the vermis superior. The anterior and posterior notches are almost obliterated, the posterior extremity of the vermis extending very nearly as far back as the level of the posterior edges of the cerebellar hemispheres. The transverse diameter of the vermis is much greater, in proportion to the whole diameter of the cerebellum, than in Man, and the vermis inferior presents no such sharp distinction into pyramid, uvula, &c., as in the human subject. The great horizontal fissure is distinct and tolerably deep; but I could discover no definite minor fissures, and consequently no demarcation of the upper, or under, surfaces of the hemispheres into lobuli. There are not even any distinct lobules, as amygdala, beside the uvula. On the other hand, the flocculi are enormous, and end in prominent rounded processes, which fit into deep fossæ upon the inner surfaces of the petrosal bones.

A distinct posterior medullary velum was visible on each side, connecting the nodule with the flocculus; and the valve of Vieussens, as usual, united the processus e cerebello ad testes. The arbor vitæ was well-marked and complex in its branchings, in a vertical median section of the cerebellum.

Of the corpora quadrigemina the nates are smaller than the testes; but the branchia superiora are larger than the branchia inferiora, on which latter the corpus geniculatum internum looks almost like a ganglion.

The pons is large and convex, but nevertheless leaves tolerably well-defined corpora trapezoidea upon the surface of the sides of the medulla oblongata, which last exhibits distinct oval olivary bodies. The pituitary body, very large and spheroidal, is connected with a prominent infundibulum, which is separated by a slight transverse notch from the single corpus mammillare.

The commissures, third ventricle, pineal gland, &c., presented nothing remarkable. The nerves are large in proportion to the brain, particularly the olfactory nerves (which are very broad and flat), the optic nerves, and the oculo-motor nerves; but beyond their large size they differ in no striking respect from the corresponding parts in Man.

EXPLANATION OF PLATE XXIX. [PLATE 36].

(All the figures are of the natural size.)

Fig. 1. Brain of *Ateles paniscus* (female), almost fresh, viewed from above.
Fig. 2. Brain of a male *Ateles*, preserved in spirit and altered in form.
Fig. 3. Under view of the female brain. The cerebellum has fallen back by its own weight beyond the posterior edges of the cerebral hemispheres. *fl.* flocculus.
Fig. 4. Side view of fig. 1.
Fig. 5. The same brain dissected, to show the lateral ventricles and their cornua. *c a*, anterior; *c d*, descending; *c p*, posterior cornu; *hippocampus minor. On the right side, the distance between the extremities of the diverging lines indicates the whole length of the cornu on one side, in the female brain.
Fig. 6. The cerebellum viewed from above; *v s*, vermis superior.
Fig. 7. The cerebellum viewed from below; *v i*, vermis inferior.

Nomenclature and Lettering of all the Figures.

Cerebrum:

Lobes: frontal lobe, *Fr*; parietal, *Pa*; median, *M*; temporal, *Te*; occipital, *Occ.*

Gyri (of the outer face):

1. Infero-frontal (étage surcilier).
2. Medio-frontal (étage frontal moyen).
3. Supero-frontal (étage frontal supérieur).
1′. Supra-orbital (plis orbitaires).
4. Antero-parietal (premier pli ascendant).
5. Postero-parietal (deuxième pli ascendant).
5′. Postero-parietal lobule (lobule du deuxième pli ascendant).
6. Angular (pli courbe).
7. Antero-temporal (pli temporal supérieur).
8. Medio-temporal (pli temporal moyen).
9. Postero-temporal (pli temporal inférieur).
10. Super-occipital (pli occipital supérieur).
11. Medio-occipital (pli occipital moyen).
12. Infero-occipital (pli occipital inférieur).
13. First external annectent
14. Second external annectent
15. Third external annectent (plis de passage externes).
16. Fourth external annectent

Gyri (of the inner face):

17. Marginal (pli de la zone externe).
18. Callosal (circonvolution de l'ourlet, Foville) (pli du corps calleux).
18′. Quadrate lobule (lobule quadrilatère, Foville).
19. Uncinate (circonvolution à crochet, V. d'Azyr) (lobule de l'hippocampe).
20. Dentate (corps godronné).
21—24. Internal annectent (plis de passage internes).
25. Internal occipital lobule (lobule occipital).

Sulci (of the outer face):

a. Infero-frontal.
b. Supero-frontal.
c. Antero-parietal.
d. Postero-parietal (scissure de Rolando, Leuret).
e. Sylvian.
f. Antero-temporal (scissure parallele).
g. Postero-temporal.
h. Temporo-occipital (scissure perpendiculaire externe).

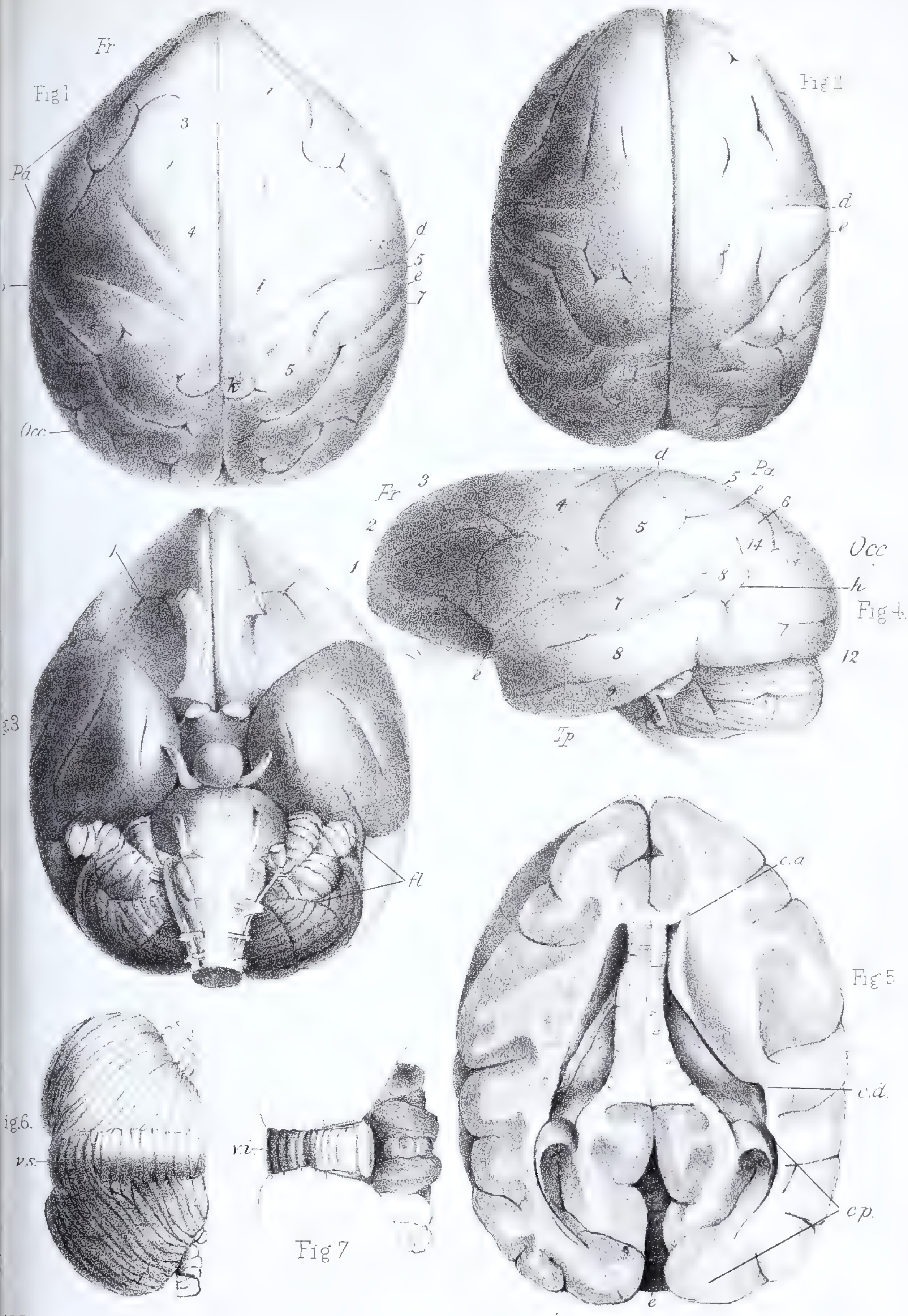
Sulci (of the inner face):

i. Calloso-marginal (grand sillon du lobe fronto-parietal).
k. Occipito-parietal (scissure perpendiculaire interne).
l. Calcarine (posterior part of the scissure des hippocampes).
m. Dentate.
n. Collateral.

ca, *cd*, *cp*, anterior, descending, and posterior cornua of the lateral ventricles.
* hippocampus minor: **hippocampus major.
ec, eminentiar collateralis, or its continuation.

[The synonyms given above are taken from the work of M. Gratiolet when no other anatomist's name is attached to them.]

P. Z. S. 1861. Plate XXIX.



West

W. West, imp.

Brain of Ateles paniscus.

XXVIII

ON FOSSIL REMAINS OF MAN

Proceedings of the Royal Institution of Great Britain, vol. iii. 1858–62, *pp.* 420—422. (*Read Friday, February* 7, 1862.)

THE purpose of the discourse was to give an explanation of the interest attaching to two casts upon the table—the one that of a skull, discovered and described by Professor Schmerling, from the Cave of Engis, in Belgium; the other, discovered by Dr. Fuhlrott and described by Professor Schaaffhausen, from a cave in the Neanderthal near Düsseldorf—the former being the oldest skull whose age is geologically definable, the latter the most aberrant and degraded of human skulls.

The nature and extent of the cranial modifications exhibited by the man-like apes and by man were discussed; and their modifications were shown to depend upon variations in the capacity and in the form of the cranium, in the greater or less development of its ridges, and in the size and form of the face. In respect of such differences, skulls have been called dolichocephalic and brachycephalic orthognathous and prognathous, &c.

Neither orthognathism nor prognathism are necessarily correlated with brachycephaly or dolichocephaly. But the most extreme prognathism is accompanied by a dolichocephalic cranium, while perfect orthognathism may occur with extreme brachycephalism.

The known varieties of the skull have a certain geographical distribution, which may be broadly expressed by drawing a line upon a map of the world from Russian Tartary to the Gulf of Guinea, and by regarding the two ends of that line as ethnological poles, while another line, drawn at right angles to it, from Western Europe to Hindostan, may be called the ethnological equator.

At the north-eastern pole are situated the people with the most eminently brachycephalic and orthognathous skulls; at the south-western pole, those people who have the most eminently dolichocephalic and prognathous skulls; while along the ethnological equator the races of men are, for the most part, oval-headed, or, if dolichocephalic, they are orthognathous. Passing from the ethnological poles, in either direction, there is a tendency to the softening down of the extreme types of skull. Turning from this general view of cranial modification, which was expressly stated to be open to many exceptions in detail, the question was next raised whether the distribution of cranial forms had been the same in all periods of the world's history, or whether the older races, in any locality, possessed a different cranial character from their successors.

No evidence of the existence of such older and different races has yet been obtained from Northern Asia, from Africa beyond the shores of the Mediterranean, or from Australia; it may be that the Alfourons and the mound-builders of the Mississippi valley are to be regarded as ancient stocks which preceded modern immigration; but definite evidence is wanting with regard to these and similar cases. In Northern and Western Europe, however, there is little doubt that several races, different in cranial conformation and in civilization, have succeeded one another. Below and beyond the traces of Roman civilization, archæologists find evidence, first, of people who used iron, then of those who employed bronze, and then of those who were acquainted only with stone and flint (or bone) weapons and implements. How far these various weapons may have been used at different epochs by the same people, is a question yet to be decided; but that in some parts of Europe, at any rate, they characterize people of different cranial structure, appears to be tolerably well made out.

The remarkable crania from tumuli of the stone period at Borreby, in Denmark, figured by Mr. Busk, were cited as authentic examples of the skulls of people of the epoch in which stone axes ground to an edge were the chief weapons.

The evidence of the antiquity of these people afforded by the peat bogs of Denmark, and the probability of their contemporaneity with the makers of the "refuse-heaps" of Denmark, and of the pile-works of Switzerland, were next considered. Ancient as the Borreby race may be, they peopled Denmark subsequently to its assumption of its present physical geography, and since its only great quadrupeds were the urus, the bison, and deer.

The Engis skull, on the other hand, is of a date antecedent to the

last great physical changes of Europe, and its owner was a contemporary of the mammoth, the tichorine rhinoceros, the cave bear, and the cave-hyæna, so that a vast gulf of time separates him from the Borreby men. The skull was shown, however, by all its measurements, to be nearly as well developed as that of an average European.

The Neanderthal skull, whose age is not exactly known, on the contrary, is the lowest and most ape-like in its characters of any human skull yet discovered, though it presents certain points of resemblance to the Borreby skulls.

Great as are the differences between the Engis, the Borreby, and the Neanderthal skulls, the speaker stated that it would not be justifiable to assign them even to distinct races of men; for by a careful examination of the crania of one of the purest of living races of men—the Australian,—it is possible to discover skulls which differ from one another in similar characters, though not quite to the same extent, as the ancient ones.

Thus it appears that the oldest known races of men differed comparatively but little in cranial conformation from those savage races now living, whom they seem to have resembled most in habits; and it may be concluded that these most ancient races at present known were at least as remote from the original stock of the human species as they are from us.

XXIX

THE ANNIVERSARY ADDRESS TO THE GEOLOGICAL SOCIETY

Quarterly Journal of the Geological Society of London, vol. xviii., 1862, pp. xl.–liv. (Delivered February 21st, 1862.)

MERCHANTS occasionally go through a wholesome, though troublesome and not always satisfactory, process which they term "taking stock." After all the excitement of speculation the pleasure of gain, and the pain of loss, the trader makes up his mind to face facts and to learn the exact quantity and quality of his solid and reliable possessions.

The man of science does well sometimes to imitate this procedure; and, forgetting for the time the importance of his own small winnings, to re-examine the common stock in trade, so that he may make sure how far the store of bullion in the cellar—on the faith of whose existence so much paper has been circulating—is really the solid gold of truth.

The Anniversary Meeting of the Geological Society seems to be an occasion well suited for an undertaking of this kind—for an inquiry, in fact, into the nature and the value of the present results of palæontological investigation; and the more so, as all those who have paid close attention to the late multitudinous discussions, in which palæontology is implicated, must have felt the urgent necessity of some such scrutiny.

First in order, as the most definite and unquestionable of all the results of palæontology, must be mentioned the immense extension and impulse given to botany, zoology, and comparative anatomy by the investigation of fossil remains. Indeed, the mass of biological

facts has been so greatly increased, and the range of biological speculation has been so vastly widened, by the researches of the geologist and the palæontologist, that it is to be feared there are naturalists in existence who look upon geology as Brindley regarded rivers. "Rivers," said the great engineer, "were made to feed canals;" and geology, some seem to think, was solely created to advance comparative anatomy.

Were such a thought justifiable, it could hardly expect to be received with favour by this assembly. But it is not justifiable. Your favourite science has her own great aims independent of all others; and if, notwithstanding her steady devotion to her own progress, she can scatter such rich alms among her sisters, it should be remembered that her charity is of the sort that does not impoverish, but "blesseth him that gives and him that takes."

Regard the matter as we will, however, the facts remain. Nearly 40,000 species of animals and plants have been added to the Systema Naturæ by palæontological research. This is a living population equivalent to that of a new continent in mere number; equivalent to that of a new hemisphere, if we take into account the small population of insects as yet found fossil, and the large proportion and peculiar organisation of many of the Vertebrata.

But, beyond this, it is perhaps not too much to say that, except for the necessity of interpreting palæontological facts, the laws of distribution would have received less careful study: while few comparative anatomists (and those not of the first order) would have been induced by mere love of detail, as such, to study the minutiæ of osteology, were it not that in such minutiæ lie the only keys to the most interesting riddles offered by the extinct animal world.

These assuredly are great and solid gains. Surely it is matter for no small congratulation that in half a century (for palæontology, though it dawned earlier, came into full day only with Cuvier) a subordinate branch of biology should have doubled the value and interest of the whole group of sciences to which it belongs.

But this is not all. Allied with geology, palæontology has established two laws of inestimable importance: the first, that one and the same area of the earth's surface has been successively occupied by very different kinds of living beings; the second, that the order of succession established in one locality holds good, approximately, in all.

The first of these laws is universal and irreversible; the second is

an induction from a vast number of observations, though it may possibly, and even probably, have to admit of exceptions. As a consequence of the second law, it follows that a peculiar relation frequently subsists between series of strata, containing organic remains, in different localities. The series resemble one another, not only in virtue of a general resemblance of the organic remains in the two, but also in virtue of a resemblance in the order and character of the serial succession in each. There is a resemblance of arrangement; so that the separate terms of each series, as well as the whole series, exhibit a correspondence.

Succession implies time; the lower members of a series of sedimentary rocks are certainly older than the upper; and when the notion of age was once introduced as the equivalent of succession it was no wonder that correspondence in succession came to be looked upon as correspondence in age, or "contemporaneity." And, indeed, so long as relative age only is spoken of, correspondence in succession *is* correspondence in age; it is *relative* contemporaneity.

But it would have been very much better for geology if so loose and ambiguous a word as "contemporaneous" had been excluded from her terminology, and if, in its stead, some term expressing similarity of serial relation, and excluding the notion of time altogether, had been employed to denote correspondence in position in two or more series of strata.

In anatomy, where such correspondence of position has constantly to be spoken of, it is denoted by the word "homology" and its derivatives; and for Geology (which after all is only the anatomy and physiology of the earth) it might be well to invent some single word, such as "homotaxis" (similarity of order), in order to express an essentially similar idea. This, however, has not been done, and most probably the inquiry will at once be made—To what end burden science with a new and strange term in place of one old, familiar, and part of our common language?

The reply to this question will become obvious as the inquiry into the results of palæontology is pushed further.

Those whose business it is to acquaint themselves specially with the works of palæontologists, in fact, will be fully aware that very few, if any, would rest satisfied with such a statement of the conclusions of their branch of biology as that which has just been given.

Our standard répertoires of palæontology profess to teach us far higher things—to disclose the entire succession of living forms upon the surface of the globe; to tell us of a wholly different distribution of climatic conditions in ancient times; to reveal the character of

the first of all living existences; and to trace out the law of progress from them to us.

It may not be unprofitable to bestow on these professions a somewhat more critical examination than they have hitherto received, in order to ascertain how far they rest on an irrefragable basis, or whether, after all, it might not be well for palæontologists to learn a little more carefully that scientific "ars artium," the art of saying "I don't know." And to this end let us define somewhat more exactly the extent of these pretensions of palæontology.

Every one is aware that Professor Bronn's 'Untersuchungen' and Professor Pictet's 'Traité de Paléontologie' are works of standard authority, familiarly consulted by every working palæontologist. It is desirable to speak of these excellent books, and of their distinguished authors, with the utmost respect and in a tone as far as possible removed from carping criticism; indeed, if they are specially cited in this place, it is merely in justification of the assertion that the following propositions, which may be found implicitly or explicitly in the works in question, are regarded by the mass of palæontologists and geologists, not only on the Continent but in this country, as expressing some of the best-established results of palæontology. Thus:—

Animals and plants began their existence together, not long after the commencement of the deposition of the sedimentary rocks, and then succeeded one another in such a manner that totally distinct faunæ and floræ occupied the whole surface of the earth, one after the other, and during distinct epochs of time.

A geological formation is the sum of all the strata deposited over the whole surface of the earth during one of these epochs: a geological fauna or flora is the sum of all the species of animals or plants which occupied the whole surface of the globe during one of these epochs.

The population of the earth's surface was at first very similar in all parts, and only from the middle of the Tertiary epoch onwards began to show a distinct distribution in zones.

The constitution of the original population, as well as the numerical proportions of its members, indicates a warmer and, on the whole, somewhat tropical climate, which remained tolerably equable throughout the year. The subsequent distribution of living beings in zones is the result of a gradual lowering of the general temperature, which first began to be felt at the poles.

It is not now proposed to inquire whether these doctrines are true

or false; but to direct your attention to a much simpler though very essential preliminary question—What is their logical basis? what are the fundamental assumptions upon which they all logically depend? and what is the evidence on which those fundamental propositions demand our assent?

These assumptions are two: the first, that the commencement of the geological record is coeval with the commencement of life on the globe; the second, that geological contemporaneity is the same thing as chronological synchrony. Without the first of these assumptions there would of course be no ground for any statement respecting the commencement of life; without the second, all the other statements cited, every one of which implies a knowledge of the state of different parts of the earth at one and the same time, will be no less devoid of demonstration.

The first assumption obviously rests entirely on negative evidence. This is, of course, the only evidence that ever can be available to prove the commencement of any series of phenomena; but, at the same time, it must be recollected that the value of negative evidence depends entirely on the amount of positive corroboration it receives. If A B wishes to prove an *alibi*, it is of no use for him to get a thousand witnesses simply to swear that they did not see him in such and such a place, unless the witnesses are prepared to prove that they must have seen him had he been there. But the evidence that animal life commenced with the Lingula-flags, *e.g.*, would seem to be exactly of this unsatisfactory uncorroborated sort. The Cambrian witnesses simply swear they "haven't seen anybody their way;" upon which the counsel for the other side immediately puts in ten or twelve thousand feet of Devonian sandstones to make oath they never saw a fish or a mollusk, though all the world knows there were plenty in their time.

But then it is urged that, though the Devonian rocks in one part of the world exhibit no fossils, in another they do, while the lower Cambrian rocks nowhere exhibit fossils, and hence no living being could have existed in their epoch.

To this there are two replies: the first, that the observational basis of the assertion that the lowest rocks are nowhere fossiliferous is an amazingly small one seeing how very small an area, in comparison to that of the whole world, has yet been fully searched: the second, that the argument is good for nothing unless the unfossiliferous rocks in question were not only *contemporaneous* in the geological sense, but *synchronous* in the chronological sense. To use the *alibi* illustration again. If a man wishes to prove he was

in neither of two places, A and B, on a given day, his witnesses for each place must be prepared to answer for the whole day. If they can only prove that he was not at A in the morning, and not at B in the afternoon, the evidence of his absence from both is *nil*, because he might have been at B in the morning and at A in the afternoon.

Thus everything depends upon the validity of the second assumption. And we must proceed to inquire what is the real meaning of the word "contemporaneous" as employed by geologists. To this end a concrete example may be taken.

The Lias of England and the Lias of Germany, the Cretaceous rocks of Britain and the Cretaceous rocks of Southern India, are termed by geologists "contemporaneous" formations; but whenever any thoughtful geologist is asked whether he means to say that they were deposited synchronously, he says "No,—only within the same great epoch." And if, in pursuing the inquiry, he is asked what may be the approximate value in time of a "great epoch"—whether it means a hundred years, or a thousand, or a million, or ten million years—his reply is, "I cannot tell."

If the further question be put, whether physical geology is in possession of any method by which the actual synchrony (or the reverse) of any two distant deposits can be ascertained, no such method can be heard of; it being admitted by all the best authorities that neither similarity of mineral composition, nor of physical character, nor even direct continuity of stratum, are *absolute* proofs of the synchronism of even approximated sedimentary strata: while, for distant deposits, there seems to be no kind of physical evidence attainable of a nature competent to decide whether such deposits were formed simultaneously, or whether they possess any given difference or antiquity. To return to an example already given. All competent authorities will probably assent to the proposition that physical geology does not enable us in any way to reply to this question—Were the British Cretaceous rocks deposited at the same time as those of India, or are they a million of years younger or a million of years older?

Is palæontology able to succeed where physical geology fails? Standard writers on palæontology, as has been seen, assume that she can. They take it for granted, that deposits containing similar organic remains are synchronous—at any rate in a broad sense; and yet, those who will study the eleventh and twelfth chapters of Sir Henry De la Beche's remarkable "Researches in Theoretical Geology," published now nearly thirty years ago, and will carry out the arguments

there most luminously stated to their logical consequences, may very easily convince themselves that even absolute identity of organic contents is no proof of the synchrony of deposits, while absolute diversity is no proof of difference of date. Sir Henry de la Beche goes even further, and adduces conclusive evidence to show that the different parts of one and the same stratum, having a similar composition throughout, containing the same organic remains, and having similar beds above and below it, may yet differ to any conceivable extent in age.

Edward Forbes was in the habit of asserting that the similarity of the organic contents of distant formations was *primâ facie* evidence, not of their similarity, but of their difference of age; and holding as he did the doctrine of single specific centres, the conclusion was as legitimate as any other; for the two districts must have been occupied by migration from one of the two, or from an intermediate spot, and the chances against exact coincidence of migration and of imbedding are infinite.

In point of fact, however, whether the hypothesis of single or of multiple specific centres be adopted, similarity of organic contents cannot possibly afford any proof of the synchrony of the deposits which contain them; on the contrary, it is demonstrably compatible with the lapse of the most prodigious intervals of time, and with interposition of vast changes in the organic and inorganic worlds, between the epochs in which such deposits were formed.

On what amount of similarity of their faunæ is the doctrine of the contemporaneity of the European and of the North American Silurians based? In the last edition of Sir Charles Lyell's 'Elementary Geology' it is stated, on the authority of a former President of this Society, the late Daniel Sharpe, that between 30 and 40 per cent. of the species of Silurian Mollusca are common to both sides of the Atlantic. By way of due allowance for further discovery, let us double the lesser number and suppose that 60 per cent. of the species are common to the North American and the British Silurians. Sixty per cent. of species in common is, then, proof of contemporaneity.

Now suppose that, a million or two of years hence, when Britain has made another dip beneath the sea and has come up again, some geologist applies this doctrine, in comparing the strata laid bare by the upheaval of the bottom, say, of St. George's Channel with what may then remain of the Suffolk Crag. Reasoning in the same way, he will at once decide the Suffolk Crag and the St. George's Channel beds to be contemporaneous; although we happen

to know that a vast period (even in the geological sense) of time and physical changes of almost unprecedented extent separate the two.

But if it be a demonstrable fact that strata containing more than 60 or 70 per cent. of species of Mollusca in common, and comparatively close together, may yet be separated by an amount of geological time sufficient to allow of some of the greatest physical changes the world has seen, what becomes of that sort of contemporaneity the sole evidence of which is a similarity of facies, or the identity of half a dozen species, or of a good many genera?

And yet there is no better evidence for the contemporaneity assumed by all who adopt the hypotheses of universal faunæ and floræ, of a universally uniform climate, and of a sensible cooling of the globe during geological time

There seems, then, no escape from the admission that neither physical geology nor palæontology possesses any method by which the absolute synchronism of two strata can be demonstrated. All that geology can prove is local order of succession. It is mathematically certain that, in any given vertical linear section of an undisturbed series of sedimentary deposits, the bed which lies lowest is the oldest. In any other vertical linear section of the same series, of course, corresponding beds will occur in a similar order; but, however great may be the probability, no man can say with absolute certainty that the beds in the two sections were synchronously deposited. For areas of moderate extent, it is doubtless true that no practical evil is likely to result from assuming the corresponding beds to be synchronous or strictly contemporaneous; and there are multitudes of accessory circumstances which may fully justify the assumption of such synchrony. But the moment the geologist has to deal with large areas or with completely separated deposits, then the mischief of confounding that "homotaxis" or "similarity of arrangement," which *can* be demonstrated, with "synchrony" or "identity of date," for which there is not a shadow of proof, under the one common term of "contemporaneity" becomes incalculable, and proves the constant source of gratuitous speculations.

For anything that geology or palæontology are able to show to the contrary, a Devonian fauna and flora in the British Islands may have been contemporaneous with Silurian life in North America, and with a Carboniferous fauna and flora in Africa. Geographical provinces and zones may have been as distinctly marked in the Palæozoic epoch as at present, and those seemingly sudden appearances of new

genera and species, which we ascribe to new creation, may be simple results of migration.

It may be so; it may be otherwise. In the present condition of our knowledge and of our methods, one verdict—"not proven, and not proveable"—must be recorded against all the grand hypotheses of the palæontologist respecting the general succession of life on the globe. The order and nature of terrestrial life as a whole are open questions. Geology at present provides us with most valuable topographical records, but she has not the means of working them up into a universal history. Is such a universal history, then, to be regarded as unattainable? Are all the grandest and most interesting problems which offer themselves to the geological student essentially insoluble? Is he in the position of a scientific Tantalus—doomed always to thirst for a knowledge which he cannot obtain? The reverse is to be hoped; nay, it may not be impossible to indicate the source whence help will come.

In commencing these remarks, mention was made of the great obligations under which the naturalist lies to the geologist and palæontologist. Assuredly the time will come when these obligations will be repaid tenfold, and when the maze of the world's past history, through which the pure geologist and the pure palæontologist find no guidance, will be securely threaded by the clue furnished by the naturalist.

All who are competent to express an opinion on the subject are at present agreed that the manifold varieties of animal and vegetable form have not either come into existence by chance, nor result from capricious exertions of creative power; but that they have taken place in a definite order, the statement of which order is what men of science term a natural law. Whether such a law is to be regarded as an expression of the mode of operation of natural forces, or whether it is simply a statement of the manner in which a supernatural power has thought fit to act is a secondary question, so long as the existence of the law and the possibility of its discovery by the human intellect are granted. But he must be a half-hearted philosopher who, believing in that possibility, and having watched the gigantic strides of the biological sciences during the last twenty years, doubts that science will sooner or later make this further step so as to become possessed of the law of evolution of organic forms—of the unvarying order of that great chain of causes and effects of which all organic forms, ancient and modern, are the links. And then, if ever, we shall be able to begin to discuss with profit the questions respecting the commencement of life, and the nature of

the successive populations of the globe, which so many seem to think are already answered.

The preceding arguments make no particular claim to novelty; indeed they have been floating more or less distinctly before the minds of geologists for the last thirty years; and if, at the present time, it has seemed desirable to give them more definite and systematic expression, it is because palæontology is every day assuming a greater importance, and now requires to rest on a basis whose firmness is thoroughly well assured. Among its fundamental conceptions, there must be no confusion between what is certain and what is more or less probable.[1] But, pending the construction of a surer foundation than palæontology now possesses, it may be instructive, assuming for the nonce the general correctness of the ordinary hypothesis of geological contemporaneity, to consider whether the deductions which are ordinarily drawn from the whole body of palæontological facts are justifiable.

The evidence on which such conclusions are based is of two kinds, negative and positive. The value of negative evidence, in connexion with this inquiry, has been so fully and clearly discussed in an address from the chair of this Society,[2] which none of us have forgotten, that nothing need at present be said about it; the more as the considerations which have been laid before you have certainly not tended to increase your estimation of such evidence. It will be preferable to turn to the positive facts of palæontology, and to inquire what they tell us.

We are all accustomed to speak of the number and the extent of the changes in the living population of the globe during geological time as something enormous; and indeed they are so, if we regard only the negative differences which separate the older rocks from the more modern, and if we look upon specific and generic changes as great changes, which from one point of view they truly are. But leaving the negative differences out of consideration, and looking only at the positive data furnished by the fossil world from a broader point of view—from that of the comparative anatomist who has made the study of the greater modifications of animal form his chief business—a surprise of another kind dawns upon the mind; and under *this* aspect the smallness of the total change becomes as astonishing as was its greatness under the other.

[1] Le plus grand service qu'on puisse rendre à la science est d'y faire place nette avant d'y rien construire."—*Cuvier*.

[2] Anniversary Address for 1851, Quart. Journ. Geol. Soc. vol. vii.

There are two hundred known orders of plants; of these not one is certainly known to exist exclusively in the fossil state. The whole lapse of geological time has as yet yielded not a single new ordinal type of vegetable structure.[1]

The positive change in passing from the recent to the ancient animal world is greater, but still singularly small. No fossil animal is so distinct from those now living as to require to be arranged even in a separate class from those which contain existing forms. It is only when we come to the orders, which may be roughly estimated at about a hundred and thirty, that we meet with fossil animals so distinct from those now living as to require orders for themselves; and these do not amount, on the most liberal estimate, to more than about ten per cent. of the whole.

There is no certainly known extinct order of Protozoa; there is but one among the Cœlenterata—that of the rugose corals; there is none among the Mollusca; there are three, the Cystidea, Blastoidea, and Edrioasterida, among the Echinoderms; and two, the Trilobita and Eurypterida, among the Crustacea; making altogether five for the great subkingdom of Annulosa. Among vertebrates there is no ordinarily distinct fossil fish: there is only one extinct order of Amphibia—the Labyrinthodonts; but there are at least four distinct orders of Reptilia, viz. the Ichthyosauria, Plesiosauria, Pterosauria, Dinosauria, and perhaps another or two. There is no known extinct order of Birds, and no certainly known extinct order of Mammals, the ordinal distinctness of the "Toxodontia" being doubtful.

The objection that broad statements of this kind, after all, rest largely on negative evidence is obvious, but it has less force than might at first be supposed; for, as might be expected from the circumstances of the case, we possess more abundant positive evidence regarding Fishes and marine Mollusks than respecting any other forms of animal life; and yet these offer us, through the whole range of geological time, no species ordinally distinct from those now living; while the far less numerous class of Echinoderms presents three, and the Crustacea two such orders, though none of these come down later than the Palæozoic age. Lastly, the Reptilia present the extraordinary and exceptional phenomenon of as many extinct as existing orders, if not more; the four mentioned maintaining their existence from the Lias to the Chalk inclusive.

Some years ago one of your Secretaries pointed out another kind of positive palæontological evidence tending towards the same conclusion—afforded by the existence of what he termed "persistent

[1] See Hooker's 'Introductory Essay to the Flora of Tasmania,' p. xxiii.

types" of vegetable and of animal life.[1] He stated, on the authority of Dr. Hooker, that there are Carboniferous plants which appear to be generically identical with some now living; that the cone of the Oolitic *Araucaria* is hardly distinguishable from that of an existing species; that a true *Pinus* appears in the Purbecks and a *Juglans* in the Chalk; while, from the Bagshot Sands, a *Banksia* whose wood is not distinguishable from that of species now living in Australia had been obtained.

Turning to the animal kingdom, he affirmed the tabulate corals of the Silurian rocks to be wonderfully like those which now exist; while even the families of the Aporosa were all represented in the older Mesozoic rocks.

Among the Mollusca similar facts were adduced. Let it be borne in mind that *Avicula*, *Mytilus*, *Chiton*, *Natica*, *Patella*, *Trochus*, *Discina*, *Orbicula*, *Lingula*, *Rhynchonella*, and *Nautilus*, all of which are existing *genera*, are given without a doubt as Silurian in the last edition of 'Siluria'; while the highest forms of the highest Cephalopods are represented in the Lias by a genus, *Belemnoteuthis*, which presents the closest relation to the existing *Loligo*.

The two highest groups of the Annulosa, Insecta and Arachnida, are represented in the Coal either by existing genera or by forms differing from existing genera in quite minor peculiarities.

Turning to the Vertebrata, the only palæozoic Elasmobranch Fish of which we have any complete knowledge is the Devonian and Carboniferous *Pleuracanthus*, which differs no more from existing Sharks than these do from one another.

Again, vast as is the number of undoubtedly Ganoid fossil Fishes, and great as is their range in time, a large mass of evidence has recently been adduced to show that almost all those respecting which we possess sufficient information are referable to the same subordinal groups as the existing *Lepidosteus*, *Polypterus*, and Sturgeon; and that a singular relation obtains between the older and the younger Fishes; the former, the Devonian Ganoids, being almost all members of the same suborder as *Polypterus*, while the Mesozoic Ganoids are almost all similarly allied to *Lepidosteus*.[2]

Again, what can be more remarkable than the singular constancy of structure preserved throughout a vast period of time by the family

[1] See the abstract of a Lecture "On the Persistent Types of Animal Life," in the 'Notices of the Meetings of the Royal Institution of Great Britain,' June 3, 1859, vol. iii. p. 151.

[2] 'Memoirs of the Geological Survey of the United Kingdom.—Decade x. Preliminary Essay upon the Systematic Arrangement of the Fishes of the Devonian Epoch.'

of the Pycnodonts and by that of the true Cœlacanths; the former persisting, with but insignificant modifications, from the Carboniferous to the Tertiary rocks, inclusive; the latter existing, with still less change, from the Carboniferous rocks to the Chalk, inclusive.

Among Reptiles, the highest living group, that of the Crocodilia, is represented at the early part of the Mesozoic epoch by species identical in the essential characters of their organization with those now living, and differing from the latter only in such matters as the form of the articular facets of the vertebral centra, in the extent to which the nasal passages are separated from the cavity of the mouth by bone, and in the proportions of the limbs.

And even as regards the Mammalia, the scanty remains of Triassic and Oolitic species afford no foundation for the supposition that the organization of the oldest forms differed nearly so much from some of those which now live as these differ from one another.

It is needless to multiply these instances; enough has been said to justify the statement that, in view of the immense diversity of known animal and vegetable forms, and the enormous lapse of time indicated by the accumulation of fossiliferous strata, the only circumstance to be wondered at is, not that the changes of life, as exhibited by positive evidence, have been so great, but that they have been so small.

Be they great or small, however, it is desirable to attempt to estimate them. Let us therefore take each great division of the animal world in succession, and whenever an order or a family can be shown to have had a prolonged existence, let us endeavour to ascertain how far the later members of the group differ from the earlier ones. If these later members, in all or in many cases, exhibit a certain amount of modification, the fact is, so far, evidence in favour of a general law of change; and, in a rough way, the rapidity of that change will be measured by the demonstrable amount of modification. On the other hand, it must be recollected that the absence of any modification, while it may leave the doctrine of the existence of a law of change without positive support, cannot possibly disprove all forms of that doctrine, though it may afford a sufficient refutation of many of them.

The *Protozoa*.—The Protozoa are represented throughout the whole range of geological series, from the Lower Silurian formation to the present day. The most ancient forms recently made known by Ehrenberg are excessively like those which now exist: no one has ever pretended that the difference between any ancient and any

modern Foraminifera is of more than generic value; nor are the oldest Foraminifera either simpler, more embryonic, or less differentiated than the existing forms.

The *Cœlenterata*.—The Tabulate Corals have existed from the Silurian epoch to the present day, but I am not aware that the ancient *Heliolites* possesses a single mark of a more embryonic or less differentiated character, or less high organization, than the existing *Heliopora*. As for the Aporose Corals, in what respect is the Silurian *Palæocyclus* less highly organized or more embryonic than the modern *Fungia*, or the Liassic Aporosa than the existing members of the same families?

The *Mollusca*.—In what sense is the living *Waldheimia* less embryonic, or more specialized, than the palæozoic *Spirifer*; or the existing *Rhynchonellæ*, *Craniæ*, *Discinæ*, *Lingulæ*, than the Silurian species of the same genera? In what sense can *Loligo* or *Spirula* be said to be more specialized or less embryonic than *Belemnites*; the modern species of Lamellibranch and Gasteropod genera than the Silurian species of the same genera?

The *Annulosa*.—The Carboniferous Insecta and Arachnida are neither less specialized nor more embryonic than those that now live, nor are the Liassic Cirripedia and Macrura; while several of the Brachyura which appear in the Chalk belong to existing genera, and none exhibit either an intermediate or an embryonic character.

The *Vertebrata*.—Among fishes I have referred to the Cœlacanthin (comprising the genera *Cœlacanthus*, *Holophagus*, *Undia*, and *Macropoma*) as affording an example of a persistent type; and it is most remarkable to note the smallness of the differences between any of these fishes (affecting at most the proportions of the body and fins, and the character and sculpture of the scales), notwithstanding their enormous range in time. In all the essentials of its very peculiar structure, the *Macropoma* of the Chalk is identical with the *Cœlacanthus* of the Coal. Look at the genus *Lepidotus*, again, persisting without a modification of importance from the Lias to the Eocene formation, inclusive.

Or among the Teleostei—in what respect is the *Beryx* of the Chalk more embryonic or less differentiated than the *Beryx lineatus* of King George's Sound?

Or to turn to the higher Vertebrata—in what sense are the Liassic Chelonia inferior to those which now exist? How are the Cretaceous Ichthyosauria, Plesiosauria, or Pterosauria less embryonic or more differentiated species than those of the Lias?

Or lastly, in what circumstance is the *Phascolotherium* more

embryonic, or of a more generalized type, than the modern Opossum; or a *Lophiodon* or a *Palæotherium*, than a modern *Tapirus* or *Hyrax*?

These examples might be almost indefinitely multiplied, but surely they are sufficient to prove that the only safe and unquestionable testimony we can procure—positive evidence—fails to demonstrate any sort of progressive modification towards a less embryonic or less generalized type in a great many groups of animals of long-continued geological existence. In these groups there is abundant evidence of variation—none of what is ordinarily understood as progression; and, if the known geological record is to be regarded as even any considerable fragment of the whole, it is inconceivable that any theory of a necessarily progressive development can stand, for the numerous orders and families cited afford no trace of such a process.

But it is a most remarkable fact, that, while the groups which have been mentioned, and many besides, exhibit no sign of progressive modification, there are others, coexisting with them, under the same conditions, in which more or less distinct indications of such a process seem to be traceable. Among such indications I may remind you of the predominance of Holostome Gasteropoda in the older rocks as compared with that of Siphonostome Gasteropoda in the later. A case less open to the objection of negative evidence, however, is that afforded by the Tetrabranchiate Cephalopoda, the forms of the shells and of the septal sutures exhibiting a certain increase of complexity in the newer genera. Here, however, one is met at once with the occurrence of *Orthoceras* and *Baculites* at the two ends of the series, and of the fact that one of the simplest genera, *Nautilus*, is that which now exists.

The Crinoidea, in the abundance of stalked forms in the ancient formations as compared with their present rarity, seem to present us with a fair case of modification from a more embryonic towards a less embryonic condition. But then, on careful consideration of the facts, the objection arises that the stalk, calyx, and arms of the palæozoic Crinoid are exceedingly different from the corresponding organs of a larval *Comatula*; and it might with perfect justice be argued that *Actinocrinus* and *Eucalyptocrinus*, for example, depart to the full as widely, in one direction, from the stalked embryo of *Comatula*, as *Comatula* itself does in the other.

The Echinidea, again, are frequently quoted as exhibiting a gradual passage from a more generalized to a more specialized type, seeing that the elongated, or oval, Spatangoids appear after the spheroidal

Echinoids. But here it might be argued, on the other hand, that the spheroidal Echinoids, in reality, depart further from the general plan and from the embryonic form than the elongated Spatangoids do ; and that the peculiar dental apparatus and the pedicellariæ of the former are marks of at least as great differentiation as the petaloid ambulacra and semitæ of the latter.

Once more, the prevalence of Macrurous before Brachyurous Podophthalmia is apparently a fair piece of evidence in favour of progressive modification in the same order of Crustacea ; and yet the case will not stand much sifting, seeing that the Macrurous Podophthalmia depart as far in one direction from the common type of Podophthalmia, or from any embryonic condition of the Brachyura, as the Brachyura do in the other ; and that the middle terms between Macrura and Brachyura—the Anomura—are little better represented in the older Mesozoic rocks than the Brachyura are.

None of the cases of progressive modification which are cited from among the Invertebrata appear to me to have a foundation less open to criticism than these ; and if this be so, no careful reasoner would, I think, be inclined to lay a very great stress upon them. Among the Vertebrata, however, there are a few examples which appear to be far less open to objection.

It is, in fact, true of several groups of Vertebrata which have lived through a considerable range of time, that the endoskeleton (more particularly the spinal column of the older genera) presents a less ossified, and so far less differentiated, condition than that of the younger genera. Thus the Devonian Ganoids, though almost all members of the same suborder as *Polypterus*, and presenting numerous important resemblances to the existing genus, which possesses biconcave vertebræ, are, for the most part, wholly devoid of ossified vertebral centra. The Mesozoic Lepidosteidæ, again, have at most biconcave vertebræ, while the existing *Lepidosteus* has Salamandroid, opisthocœlous, vertebræ. So, none of the Palæozoic Sharks have shown themselves to be possessed of ossified vertebræ, while the majority of modern Sharks possess such vertebræ. Again, the more ancient Crocodilia and Lacertilia have vertebræ with the articular facets of their centra flattened or biconcave, while the modern members of the same group have them procœlous. But the most remarkable examples of progressive modification of the vertebral column, in correspondence with geological age, are those afforded by the Pycnodonts among fish, and the Labyrinthodonts among Amphibia.

The late able ichthyologist Heckel pointed out the fact, that, while the Pycnodonts never possess true vertebral centra, they differ in the

degree of expansion and extension of the ends of the bony arches of the vertebræ upon the sheath of the notochord; the Carboniferous forms exhibiting hardly any such expansion, while the Mesozoic genera present a greater and greater development, until, in the Tertiary forms, the expanded ends become suturally united so as to form a sort of false vertebra. Hermann von Meyer, again, to whose luminous researches we are indebted for our present large knowledge of the organization of the older Labyrinthodonts, has proved that the Carboniferous *Archegosaurus* had very imperfectly developed vertebral centra, while the Triassic *Mastodonsaurus* had the same parts completely ossified.[1]

The regularity and evenness of the dentition of the *Anoplotherium* as contrasted with that of existing Artiodactyles, and the assumed nearer approach of the dentition of certain ancient Carnivores to the typical arrangement, have also been cited as exemplifications of a law of progressive development, but I know of no other cases based on positive evidence which are worthy of particular notice.

What then does an impartial survey of the positively ascertained truths of palæontology testify in relation to the common doctrines of progressive modification, which suppose that modification to have taken place by a necessary progress from more to less embryonic forms, or from more to less generalized types, within the limits of the period represented by the fossiliferous rocks?

It negatives those doctrines: for it either shows us no evidence of any such modification, or demonstrates it to have been very slight; and as to the nature of that modification, it yields no evidence whatsoever that the earlier members of any long-continued group were more generalized in structure than the later ones. To a certain extent, indeed, it may be said that imperfect ossification of the vertebral column is an embryonic character; but, on the other hand, it would be extremely incorrect to suppose that the vertebral columns of the older Vertebrata are in any sense embryonic in their whole structure.

Obviously, if the earliest fossiliferous rocks now known are coeval with the commencement of life, and if their contents give us any just conception of the nature and the extent of the earliest fauna and flora, the insignificant amount of modification which can be demonstrated to have taken place in any one group of animals

[1] As this Address is passing through the press (March 7, 1862), evidence lies before me of the existence of a new Labyrinthodont (*Pholidogaster*), from the Edinburgh coal-field, with well-ossified vertebral centra.

or plants is quite incompatible with the hypothesis that all living forms are the results of a necessary process of progressive development, entirely comprised within the time represented by the fossiliferous rocks.

Contrariwise, any admissible hypothesis of progressive modification must be compatible with persistence without progression through indefinite periods. And should such an hypothesis eventually be proved to be true, in the only way in which it can be demonstrated, viz., by observation and experiment upon the existing forms of life, the conclusion will inevitably present itself, that the Palæozoic, Mesozoic, and Cainozoic faunæ and floræ, taken together, bear somewhat the same proportion to the whole series of living beings which have occupied this globe, as the existing fauna and flora do to them.

Such are the results of palæontology as they appear, and have for some years appeared, to the mind of an inquirer who regards that study simply as one of the applications of the great biological sciences, and who desires to see it placed upon the same sound basis as other branches of physical inquiry. If the arguments which have been brought forward are valid, probably no one, in view of the present state of opinion, will be inclined to think the time wasted which has been spent upon their elaboration.

XXX

ON NEW LABYRINTHODONTS FROM THE EDINBURGH COAL-FIELD.

Quarterly Journal of the Geological Society of London, vol. xviii., 1862, *pp.* 291-296. (*Read May 7th*, 1862.)

PLATE XI. [PLATE 37].

1. *Note respecting the Discovery of a new and large Labyrinthodont* (Loxomma Allmanni, *Huxley*) *in the Gilmerton Ironstone.*

DURING my visit to Edinburgh in January last, my friend Professor Allman, becoming aware that I was engaged in collecting materials for the study of the genus *Rhizodus* (Owen), very liberally granted me free access to the large collection of vertebrate fossils from Burdie House and Gilmerton, in the Museum of the University.

I thus became acquainted, for the first time, with the upper and under aspects of the head, and with the indubitable scales of this remarkable fish; and, putting the information thus obtained with that derived from the study of specimens in many other collections, I am now in a position to prove that *Rhizodus* is one of the cycliferous Glyptodipterini.

But, while looking through the large series of remains from the Gilmerton ironstone in the Edinburgh Museum, most of which are referable to *Rhizodus*, I came upon two or three specimens of a very different character. The most important and significant of these is the fragment of the hinder part of the upper wall of a large cranium (Pl. XI. [Plate 37] fig. 1) presenting its smooth inner, or under, surface to the eye. Where the substance of the bone has been broken away, however, the impressed surface of the matrix shows that the outer, or upper surface was ornamented with strong inosculating ridges separated by intermediate grooves. The serrated sutures of the bones com-

posing this fragment of a skull are, for the most part, distinctly traceable, and prove it to be composed of two quadrate, supraoccipital elements with two elongated parietal bones, the apposed edges of which are deeply notched at the junction of their middle with their posterior third, so as to give rise to a rounded parietal foramen, $\frac{3}{10}$ths of an inch wide. The parietals unite, in front, with a pair of frontals which are narrow behind, but expand anteriorly, and then become broken and disfigured. An arcuated postfrontal is connected with the posterior moiety of the outer edge of each frontal, and with the antero-external edge of the parietal. Externally, its smooth, almost vertically bevelled, margin bounds the inner and posterior part of the orbit. The latter cavity has an irregularly oval shape, the long axis of the oval being directed, from without and in front, obliquely inwards and backwards, at an angle of about 45° with the long axis of the skull. The anterior and outer part of the wall of the orbit is broken away; but, internally, it is bounded by a stout prefrontal, on the under face of which is the indication of a ridge, now broken away, but which once projected towards the palate. The prefrontal joins the postfrontal and, just in front of the junction, expands, somewhat suddenly, outwards, so as to form a sort of promontory which disturbs the even contour of the orbit on its inner side.

The postero-lateral boundary of the orbit is formed, in its hinder half, by a postorbital bone, and, in its anterior half, by what appears to be the jugal bone. All that remains of the outer boundary is a trihedral bar of bone 0·5 inch wide, which I take to be the hinder part of the maxilla, though it may be the continuation, forwards, of the jugal. This bony bar is concave on its outer or upper surface, which is coarsely sculptured, while its inner and outer surfaces slope towards one another, so as to form an edge below, which is sharp in front and gradually dies away behind. The outer face is flat, and exhibits a delicate rugose sculpture: the inner is slightly excavated.

Behind the orbit the lateral part of the roof of the cranium widens, and is produced, at its external and posterior angle, into a broad, expanded, and irregularly shaped plate, whose extreme outer point is broken away. In consequence of the projection of this plate beyond the general contour of the skull, the lateral margin of the latter curves suddenly outwards, midway between the orbit and the postero-lateral extremity, and then passes into the straight outer edge of the plate in question. This plate appears to be mainly formed by the quadrate and squamosal bones. Internally it presents a curved contour, convex inwards, which sweeps round when it reaches the

posterior margin of the skull, and then passes backwards into the lateral boundary of the epiotic bone. The posterior contour of the skull consequently presents a deep notch between the epiotic bone and the plate in question. The epiotic bone, small and pointed posteriorly, is wedged in between the supraoccipital element, the parietal, and the squamosal.

The description here given refers chiefly to the right (proper) half of the skull. The left half is broken away, so as to leave only the left supraoccipital, the left parietal, and part of the left frontal and postfrontal. The complete preservation of the latter bone fortunately enables one to form an accurate judgment of the minimum width of the interobital space.

The structure of the cranial fragment which has been described proves it, without doubt, to belong to a Labyrinthodont Amphibian, and affords sufficient evidence of the character of the whole skull. The straightness of what remains of the external edge renders it probable that the skull was elongated, like that of *Archegosaurus*; and on completing the left side of the posterior part of the skull by the aid of the right side, and restoring the general contour on the basis of *Archegosaurus*, we get a diagram of the whole skull which is probably not very far removed from the truth.

Posteriorly the skull had a width of 10¼ inches; and if the snout were even less acute than that of *Archegosaurus*, its total length would be about 14 inches. The largest *Archegosaurus* skull known does not exceed 12 inches in length.

From the skull of *Archegosaurus*, and from that of all other Labyrinthodonts at present known, the present specimen is distinguished by the proportional size, backward position, form and very oblique disposition of the long axis of the orbits. And as the orbits of species of known genera of Labyrinthodonts do not differ from one another in any essential respect, I conceive this character to be of generic importance; and I propose the name of *Loxomma* for the new genus thus characterised. The species may be termed *Loxomma Allmanni*, after the eminent Professor of Natural History in the University of Edinburgh, who aided me so essentially in discovering it.

The skull, however, was not the first relic of this interesting Amphibian which came to light. What, in fact, originally led me to divine the existence of a large new Labyrinthodont in the Scotch coal-field, was the discovery of a rhomboidal plate of bone so extremely similar to the middle sternal plate of a Labyrinthodont as at once to awaken suspicion. Subsequently I found another speci-

men, exhibiting this median plate with the triangular lateral plates, which are connected with its antero-lateral edges in Labyrinthodonts *in situ*. This specimen is represented in fig. 2.

The median plate is $5\frac{3}{4}$ inches long, by at least $2\frac{1}{4}$ inches broad at its widest part. Its anterior extremity is broken away, but, I think, not for any great extent. Its posterior end (almost entire) is abruptly truncated, and $\frac{3}{4}$ of an inch wide. It continues of about the same width for nearly an inch, and then its edges, becoming thinner, sweep outwards with a slight curve until the plate attains the maximum width I have mentioned, at a distance of $2\frac{1}{2}$ inches from its hinder end. Here it becomes so completely overlapped by the lateral plates, that no more can be said about its lateral contour. A fragment of a somewhat larger plate of the same kind leads me to believe, however, that the plate does not attain any much greater width anteriorly. The middle of the plate is thicker than its edges; and shallow, slightly reticulated grooves diverge from the concealed centre of the plate, towards its thin edges, before reaching which they are lost. The form of what remains of the lateral plates is given in the figure; they are thicker internally and exhibit the same radiating grooved sculpture as the median plate. The grooves diverge from the middle of the inner margin of each plate.

2. *Description of a new Labyrinthodont* (Pholidogaster pisciformis, *Huxley*).

Loxomma is not the only Labyrinthodont in the Edinburgh coal-field. Some years ago a remarkable fossil was obtained from the same district by Sir Philip Egerton and the Earl of Enniskillen, but as, on mature consideration, it appeared to them not to be a fish, it was handed over to the British Museum. My attention was long ago drawn to this specimen by Mr. Davis, of that Institution, who, at the same time, very justly remarked upon the resemblance in the arrangement of the scales between this animal and *Archegosaurus*.

A recent careful study of the fossil has fully borne out Mr. Davis's suspicion, and has convinced me that the fossil is an Amphibian allied to *Archegosaurus*, though it differs from the latter in the form of the head, the extent to which the ossification of the vertebral column has proceeded, and in the characters of its dermal armour. It shares with *Archegosaurus*, however, the peculiarity of having its overlapping scales arranged in double oblique series between the pectoral and pelvic arches only, whence, and on account of its fish-like form,

I propose the name of *Pholidogaster pisciformis* for the genus and species.

The specimen (Pl. XI. [Plate 37] fig. 3) is in a very indifferent state of preservation, and is so disposed in the matrix as to show the under or ventral surface of the head and body. Its total length is about 43 or 44 inches, of which the head occupies less than $\frac{1}{6}$th, the ramus of the lower jaw being 7 inches long. At its hindmost or widest part, the head measures about 5 inches in transverse diameter. In shape it resembles an oval bisected along its short diameter, the snout being completely rounded off. In front of the symphysis of the mandible, the under surface of the premaxilla is visible, bearing the stumps of two teeth. These teeth are situated at some distance (about 0·7 of an inch) from the middle line, and pass outside the ramus of the mandible. They are conical, and round in transverse section. Neither is entire ; but the fragment on the right side is the longer (0·2 inch), and is slightly curved, its convexity being directed forwards. The basis of the teeth are marked by strong longitudinal grooves.

The right ramus of the mandible is better shown than the left, though both rami are more or less distorted and crushed. The angular piece is large, and has the form and sculpture common among Labyrinthodonts.

Between the hinder parts of the rami of the mandible, but nearer the left than the right, are two bony plates, having the form of right-angled triangles, with their bases backwards and their perpendiculars directed inwards, close to and parallel with one another. More of the right plate is visible than of the left, and its outer angle is seen to be produced into a process which is bent at a right angle towards the dorsal side of the body. A coarse sculpture, consisting of ridges which radiate fanwise from the outer angle of each plate towards its inner edge, and anastomose, so as to leave elongated pits, marks the surface of these plates.

I conceive that these correspond with the lateral thoracic plates of the Labyrinthodonts, thrown out of their proper places and approximated, so as to hide the anterior half of the lozenge-shaped median plate, distinct traces of the posterior half of which plate appear to me to be still visible.

The ventral armour commences behind these thoracic plates, and forms an oblong sheet of scales, about 4 inches broad and 17 inches long, while each scale may measure half an inch long by ·15 broad. When the scales are well preserved and separately distinguishable, they are seen to be somewhat oat-shaped, the outer end being much

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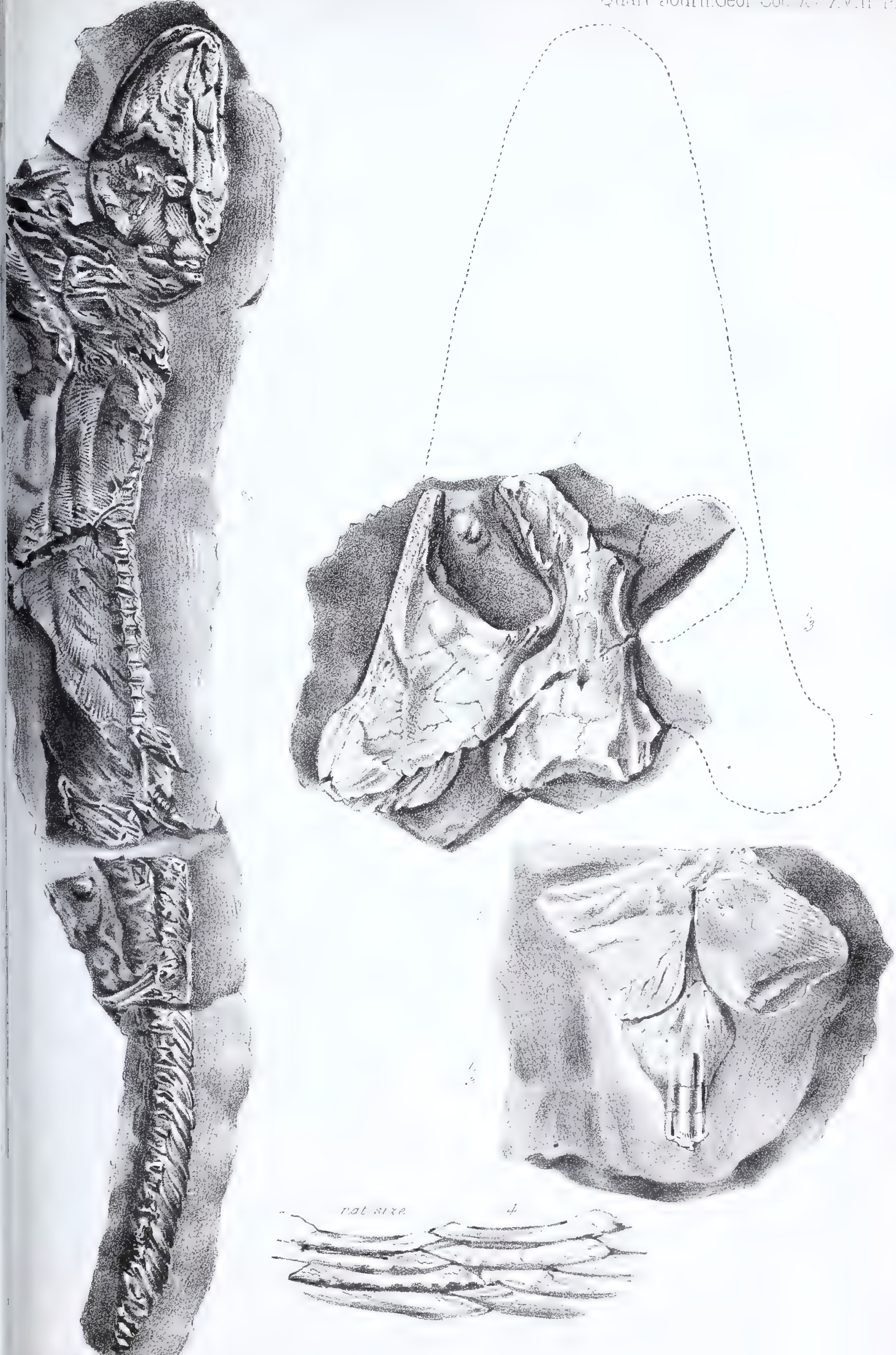

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CARBONIFEROUS LABYRINTHODONTS

W West, imp.

more obtuse in some scales than in others. The scale is thick, and rises to a sort of ridge in the middle. The inner end of its outer face is commonly bevelled off, or grooved, so as to receive the outer end of the next scale in front of and internal to it. The scales are so arranged as to form oblique series, directed inwards and forwards, and meeting in the middle line.

Posteriorly (fig. 4) the scales seem to become longer, so as to assume a bar-like character ; and at the extreme posterior end of the shield there are two irregular, broad, flat plates, apparently bony, and each rather more than half an inch wide. The structure of the fossil is here, however, very obscure.

Vertebral centra become distinctly visible on the left side of the posterior third of the dermal shield. None of them are completely exposed ; but, from what appears, they measure rather less than half an inch antero-posteriorly, and a little more in a direction at right angles to this. They are well ossified, slightly constricted in the middle and have either flat or biconcave articular ends—probably the latter. The under surface, which is exposed, exhibits a median ridge and two lateral depressions.

The characters of the neural arches can nowhere be distinctly made out, though well-marked traces of them are discernible, particularly in the caudal region, where indications of subvertebral arches, or chevron-bones, are also to be found.

At a distance of about 19 inches from the hinder end of the ramus of the mandible, and about 17 inches from the end of the tail, a stout bone, 1·6 inch long, broad at each end and thinner in the middle, lies obliquely across the axis of the body. Its vertebral end is half an inch wide, and has a well-marked, though shallow, groove or longitudinal depression on its outer surface. An oval depression, filled with matrix, occupies the anterior face of the opposite end of this bone. There are fragments of one or two other long bones behind this ; and the ventral armour, which ends about an inch in front of the bone described, is connected posteriorly, as I have stated above, with two much-broken, broad, thin, bony plates.

I take these parts to be the remains of the pelvic girdle and member, though their condition is such as to render it almost impossible to decipher their precise nature.

DESCRIPTION OF PLATE XI. [Plate 37].

Fig. 1. Cranium of *Loxomma Allmanni*, one-third the natural size.

Fig. 2. Median and lateral sternal plates of the same Labyrinthodont.

Fig. 3. *Pholidogaster pisciformis*, one-fifth the natural size.

Fig. 4. Scales of *Pholidogaster*, of the natural size.

XXXI

ON A STALK-EYED CRUSTACEAN FROM THE CARBONIFEROUS STRATA NEAR PAISLEY.

Quarterly Journal of the Geological Society of London, vol. xviii., 1862, *pp.* 420–422. (*Read June* 18*th*, 1862.)

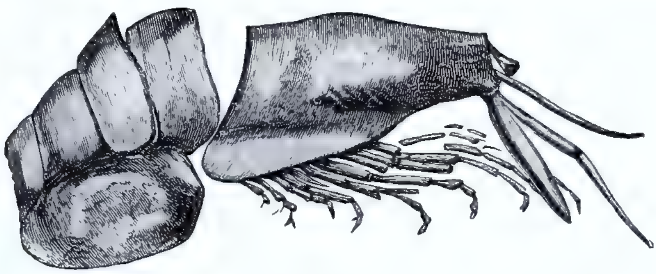
In a paper published in the Geological Society's 'Journal' (vol. xiii. p. 363, 1857), I described several specimens of a Stalk-eyed Crustacean, from the rocks of carboniferous age, to which I applied the generic name of *Pygocephalus*, referring the genus to either the Decapodous or Stomapodous group of the Class.

My friend and colleague, Mr. Geikie, F.G.S., has been so good as to draw my attention to what I believe to be another specimen of the same Crustacean, obtained by the Rev. Mr. Fraser, M.A., from one of the coal and ironstone mines in the Strath of the Clyde, about two miles from Paisley, in dark shale,[1] and by the obliging permission of its owner, has placed it in my hands for examination and description. I say I *believe* the new fossil to be another specimen of *Pygocephalus*, because in consequence of the different position in which the present specimen is imbedded in the matrix, a strict comparison with the others is almost impossible; and my determination is based rather on general analogy of the forms than on a complete identification.

While the other specimens presented a view of the ventral surface, this shows the lateral aspect of the animal, exhibiting a side-view of the carapace, of the thoracic and some of the cephalic appendages, and of the large and curved abdomen. The carapace, the

[1] "This dark shale," says Mr. Fraser, in a letter to me, "is about 19 fathoms below the surface. The ironstone-clay-band lies about 7 fathoms above it; and 36 fathoms beneath it, occurs what is known here as the Hurlet or Nitshill Coal."

lateral surface of which is convex from above downwards, is narrow and apparently truncated in front, but deep behind, its postero-inferior angle being somewhat produced, but rounded off. It measures 0·65 in. in extreme length, 0·3 in. in extreme depth. The dorsal walls of the abdominal *somites*, of which only the anterior three or four are clearly distinguishable from one another, are large in proportion to the carapace, having a depth of 0·3 in., and an antero-posterior length of 0·13 in. The free inferior edges are not clearly defined, but their margins seem to have had much the same curvature as those of *Astacus* or *Homarus*. The first obvious abdominal segment is separated from the carapace by an interval, in which I think I can trace the remains of the small, true, first abdominal segment, not much more than half the size of the others. If this be the case, then the dorsal parts of the fifth and sixth *somites* are broken away; and all that remains of the telson and the appendages of the



Sketch of Pygocephalus (?) *from the Coal-shale near Paisley.*

sixth *somite* is a broad flat plate, which lies in front of the third and fourth abdominal *somites*.

I explained in my previous paper the difficulties which I met with in endeavouring to understand this part of the body of *Pygocephalus*; and I am sorry to say that the new specimen casts but little light upon the subject. The appendages are fairly displayed. At the anterior part of the carapace I believe I can discern the eye-stalk, which is about 0·1 in. long, broader at its free than at its attached end, and exhibits a depression, which is broad in front but narrows behind to a point on the outer side of its distal half. This depression appears to result from the more yielding character of the integument, that investing the rest of the eye-stalk being dense and shining; and the surface of this softer integument is distinctly facetted. The character of the appendage, in short, closely agrees with that of the dried eye-stalk of a Podophthalmous Crustacean. Behind and below the eye-stalk the remains of the antennule are traceable; and this is succeeded by the antenna,

its great basal scale being very largely developed. Behind these follow about seven slender, filiform, jointed limbs, diminishing in length from before backwards ; indistinct traces of a second division, or *exopodite*, are discernible in these limbs.

Notwithstanding the imperfect condition of this new specimen, and the very little that it enables me to add to what was already known of *Pygocephalus*, it is so desirable to call the attention of collectors to the various aspects under which the higher *Crustacea* make their appearance in the oldest rocks at present known to contain them, that I venture to communicate the present notice to the Geological Society.

XXXII

ON THE PREMOLAR TEETH OF DIPROTODON, AND ON A NEW SPECIES OF THAT GENUS.

Quarterly Journal of the Geological Society of London, vol. xviii., 1862, *pp.* 422–427. (*Read June* 18*th*, 1862.)

PLATE XXI. [PLATE 38].

A SHORT time since, I was requested by Dr. Cotton, F.G.S., to examine a series of Australian fossils in his collection, which were procured by Mr. Isaacs from Gowrie, in the district of the Darling Downs in Queensland, the same locality from which other specimens in the Hunterian and British Museums were obtained. These fossils consisted of numerous teeth and fragments of jaws of *Macropus Atlas* and *M. Titan:* part of the upper jaw of a new species of Kangaroo, as large as these, but allied to *Lagorchestes* and *Hypsiprymnus*; with three lumbar vertebræ, a sacrum, portions of two innominate bones, three ossa calcis, and a right metatarsal of the great toe, belonging to these Marsupials. The metatarsal is remarkable for its short and stout proportions. But the most interesting among these remains were fragments of *Diprotodon*, comprising sundry molar teeth, a small portion of the right ramus of a lower jaw and parts of the right and left upper jaws of two distinct individuals. Of these upper jaws, the former, which I shall call No. 1 (Pl. XXI. [Plate 38] fig 1.), contained the premolar in place and the socket of the succeeding molar, with one fang in place. Fortunately among the detached teeth, I found the crown and principal fang of this molar, and the premolar of the other side of the same skull. The other or left upper jaw, No. 2 (fig. 4), has a very different colour and texture, from the nature of the ferruginous matrix in which it has been imbedded. It retains a part of the palatine plate, and holds three teeth—the premolar and first and second molars. What (from its aspect and

mineral condition) I do not doubt to be the fourth or hindermost, molar of the same series was found loose among the other teeth.

The genus *Diprotodon* was founded by Professor Owen[1] upon part of a lower law, collected by Sir Thomas Mitchell, from a cave in the Wellington Valley. In 1845 further details were given by the same author,[2] who described two fragments of lower jaws, and all the lower series of teeth but the premolar. Of this tooth all that is said is, "its socket shows that it was implanted, like the other molars, by two fangs" (*l. c.* p. 214). A dorsal vertebra and a calcaneum, from the same deposits, are provisionally ascribed to the same genus.

In the "Catalogue of the Fossil Organic Remains of *Mammalia* and *Aves* in the Museum of the Royal College of Surgeons" (1855), Professor Owen has given a fuller description, accompanied by figures, of the previously known remains of *Diprotodon australis*, and has added an account of some fragments of ribs, scapulæ, and limb-bones. No portions of the upper jaw, or of its teeth, are described in these successive communications; but in the paper "On some outline drawings and photographs of the skull of the *Zygomaturus trilobus*" (Quart. Journ. Geol. Soc. 1859, p. 168), it is stated of "*Zygomaturus*," —"By the dentition of the upper jaw this fossil agrees in that essential character with the genus *Diprotodon*" (p. 173); and further, at p. 175, "The bony palate appears to have been entire or without any unusually large palatal vacuity, in this respect resembling the same part in *Macropus major* and *Diprotodon*;" and again at p. 175, —"In the cranium of *Diprotodon* in the Sydney Museum, of which photographs have been transmitted to me by Mr. George Bennett, the number of molar teeth is reduced to eight, four on each side, but it is by the loss of the first small molar; and from the appearance of that molar in *Zygomaturus*, I conjecture that it would also be shed in an older individual. But there are specimens in both the British Museum and the Hunterian Museum which demonstrate that the *Diprotodon* has five molar teeth developed on each side of both upper and lower jaws, as stated in my 'Report on the extinct Mammals of Australia.'"

I may remark, incidentally, that I am unable to find any reference to the upper jaw in the 'Report' here cited. In the passage which immediately precedes that just quoted, Professor Owen says,—"I

[1] Mitchell's 'Three Expeditions into the Interior of Eastern Australia,' vol. ii. p. 368, pl. 9. fig. 1. 1838.

[2] Report of the Meeting of the British Association for 1844, p. 223; 'Report on the Extinct Mammals of Australia, &c.,' by Prof. Owen, F.R.S.

have to state that the British Museum has now received ample evidence that the generic distinction which Mr. MacLeay believes to exist between that fossil (*Zygomaturus*) and *Diprotodont* is not present."

My valued friend Mr. MacLeay, however, by no means made the mistake here attributed to him, of establishing a new genus unnecessarily. "*Zygomaturus*" *is*, without doubt, generically distinct from *Diprotodon*: indeed, Mr. MacLeay's conclusion is implicitly admitted by Professor Owen in the paper which follows that cited above, and which is chiefly devoted to an attempt to prove the identity of *Zygomaturus* (MacLeay) with *Nototherium* (Owen); for the latter genus is regarded by Professor Owen as perfectly distinct from *Diprotodon*.

In the plate (Plate IX) which accompanied that communication, the left penultimate upper molar of *Diprotodont* is figured (fig. 6); and the transverse direction of the principal ridges, as contrasted with their oblique direction in *Nototherium*, is noted.

I have now, I believe, adverted to all that has been written regarding the dentition of *Diprotodon*; and it will be observed that much remains to be learned respecting the premolar teeth and the dentition of the upper jaw generally. I shall proceed, therefore, to describe, at some length, the fossils noted above as Nos. 1 and 2.

No. 1 (Pl. XXI. [Plate 38] figs. 1, 2, 3). This consists of so much of the right maxilla of a *Diprotodon* as would lie between an anterior boundary-line, drawn through the anterior end of the infraorbital canal and the alveolar margin, half an inch in front of the premolar, and a posterior boundary-line, drawn at right angles to the alveolar margin, between the fangs of the first molar tooth. The superior limit of the fragment is the commencement of the lacrymal or antorbital prominence. The distance between the alveolar margin and the latter is 3 inches. The outer surface of the maxilla is strongly inclined inwards below the suborbital foramen, flattened or slightly convex from the alveoli of the premolar and molar to the level of that foramen, and slopes backwards and inwards, so as to be markedly concave above that point. Although not more than an inch and a half of the infraorbital canal is preserved, its anterior end is fully half an inch below its posterior extremity, so strongly is it inclined downwards and forwards.

In all these characters the fossil agrees with *Diprotodon*, and differs from *Zygomaturus*[1]; in which latter animal the surface of

[1] I employ Mr. MacLeay's generic name *Zygomaturus* for the fossil skull which he originally described, because, until a lower jaw has been discovered in connexion with such a skull, and that lower jaw turns out to be generically identical with the mandible upon which Professor Owen founded his genus *Nototherium*, the identity of *Nototherium* and *Zygomaturus* cannot be considered to be proved.

the maxilla slopes directly outwards and backwards from the infraorbital foramen to form the prominent anterior margin of the orbit. In *Zygomaturus* the zygomatic process of the maxilla is given off at a point where the surface of that bone is quite smooth in the fossil before us.

Of No. 2 (Pl. XXI. [Plate 38] figs. 4, 5, 6), a left maxilla, less of the upper and anterior, and more of the posterior and inner part, remain. The floor of the infraorbital foramen remains, and exhibits the same rapid slope as that of the other specimen. A strong horizontal palatine process is given off from the inner side of this fragment of the left maxilla. Its greatest breadth is one inch and three-eighths; and its inner boundary, rough and broken, presents no indication of a suture, so that the palate had more than double this width at this point. Opposite the interval between the first and second molars a small canal opens forwards, upon the under and anterior surface of the palate opposite the premolar. The palatine plate is three-eighths of an inch thick, and presents a flat external division, separated by a ridge from an inner part which slopes somewhat upwards; but behind the opening of the canal just mentioned, the under or oral surface rises both inwards and backwards; and the upper or nasal surface falling in the same proportion, the palatine plate ends posteriorly and internally, opposite the interval between the second and third molars, in a thin edge, which, in this specimen, is nowhere completely entire. In a specimen of the right maxilla of *Diprotodon*, containing all the teeth save the premolar, in the collection of the British Museum (marked 32858), to which I shall have occasion to make frequent reference, the palatine plate is seen to end in a free, thin, rounded edge, and to become narrower from the level of the commencement of the third molar; so that, no doubt, a great palatine vacuity existed at this spot. This is the more remarkable, as, judging from a cast in the same collection, the palate of *Nototherium* was entire, and extended, as in the Kangaroos, behind the last molar tooth.

The molar teeth have the general characters of those of the lower jaw of *Diprotodon* already described by Professor Owen. Each exhibits two principal transverse ridges, with a posterior almost obsolete, and an anterior, much more prominent and thick, but still low, basal ridge. The principal ridges are directed transversely to the axis of the palate and the alveolar margin, or have, at most, but a very slight inclination backwards and inwards. They are slightly concave backwards; and they wear down at first into two oval or elongate-reniform facets, separated by a deep valley, whose outer ends are, as usual, higher than the inner. The tooth becomes abraded faster in front than behind,—the anterior basal ridge contributing a single

or double strip-like facet, which becomes connected in the middle with the worn face of the anterior of the two principal ridges. The latter also eventually unite in the middle of the tooth ; so that, in much-worn teeth, the broad, four-sided field of dentine is surrounded only by a narrow band of enamel, the lateral portions of which present two sharply re-entering angles. There is no cinulum continued upon either the outer or the inner sides of the base of these teeth. The surface of the enamel has that sort of "reticulo-punctate or worm-eaten" look which is mentioned by Professor Owen as characteristic of the teeth in this genus.

The first molar is rather smaller than the second : the third is wanting : the fourth is considerably longer than the second, as the measurements given below will show, and has not the square outline of the first and second ; but it diminishes posteriorly by the incurvation of its outer contour. Hence the posterior transverse ridge of the fourth molar is much smaller than the anterior. The tooth is not at all worn, and seems to have been but just cut. The principal crests are excavated from side to side posteriorly, and are correspondingly convex anteriorly. Superiorly they rise to a minutely ridged and forwardly curved edge, which is slightly concave upwards. The anterior basal ridge is sharply defined, but is not so thick as in the second molar.

Each molar tooth has a single posterior fang and two anterior fangs.

The premolar tooth (not more than half the size of the molar which succeeds it, and very much less worn) differs somewhat in its characters in the two fossils. I will first describe it as it appears in No. 1, where the premolar teeth of both sides are preserved. The tooth is implanted by two fangs, an anterior, smaller, and a posterior, larger ; and its crown has somewhat the form of a tetrahedron with a truncated apex. The posterior side is flat, and slopes obliquely forwards to the roof-like summit of the tooth. The outer convex surface (fig. 1), is divided into three minor vertical convexities by two shallow grooves, which cease about halfway towards the base of the crown. The inner surface (fig. 3), less extensive than the outer, is convex and triangular, being narrower towards the summit of the crown. It passes gradually into the anterior side, which is also triangular, but still narrower. From the vertical depressions on the outer surface two grooves extend inwards on to the crown, which is thus divided by two transverse valleys separated by elevations. Of these, the two posterior, broad and ridge-like, join internally to form the inner surface of the tooth ; while the anterior, which has more the

form of a cone than that of a crest, is not more than half as broad as the others, and terminates, internally, in a smoothly rounded convex pillar, which remains distinct to the base of the crown. From its anterior surface a ridge springs, which, gradually decreasing in height, skirts its base and then ascends, upon the inner part of the middle ridge, to form the anterior boundary of the inner face of the tooth. The posterior basal ridge is well marked and concave upwards; its inner and outer ends, as it were, ascending upon the postero-external and postero-internal angles of the tooth. The anterior, or mammillary, elevation is not at all worn in either tooth. The middle and posterior ridges are slightly worn, so as to give rise to two elongated facets, each not more than one-sixth of an inch wide, and passing into one another internally, being separated only by the posterior groove, which dilates somewhat suddenly at its inner end (fig. 2).

The premolar of No. 2 is constructed upon precisely the same general plan as that of No. 1, but differs in several details. Thus, it is slightly smaller, and the antero-internal ridge which skirts the base of the mammilla has a somewhat different form. But the most marked difference is offered by the outer surface of the tooth (fig. 4), which presents not merely three smoothly convex surfaces, as in the other specimen, but exhibits three well-defined vertical ridges, connected by prominent, curved, basal elevations. The premolar of this specimen is altogether somewhat smaller than that of the other.

That both these specimens are specifically distinct from the only species of *Diprotodon* known at present, viz. *D. australis*, appears likely, at first sight, from a comparison of the dimensions of the corresponding teeth.

In the maxilla of *Diprotodon australis* (British Museum, No. 32848), to which I have already referred, the socket of the premolar and the first and second molars occupy a space of 4½ inches in the alveolar margin of the maxilla: in No. 2 the same teeth occupy only about 3½ inches. The measurements of the individual teeth, given in eighths of an inch in the following table, present a nearly similar ratio.

	No. 2.		No. 1.		*D. australis* (B.M).	
	Breadth.	Length.	Breadth.	Length.	Breadth.	Length.
Premolar	6½	7½	7	8	5	8[1]
First molar	9½	10	12	10	13	12
Second molar	11½	12	...	...	16	15
Fourth molar	13	16	...	...	17	20

[1] These are measurements of the alveolus and its contained fang. The crown of the tooth was doubtless much larger in each dimension.

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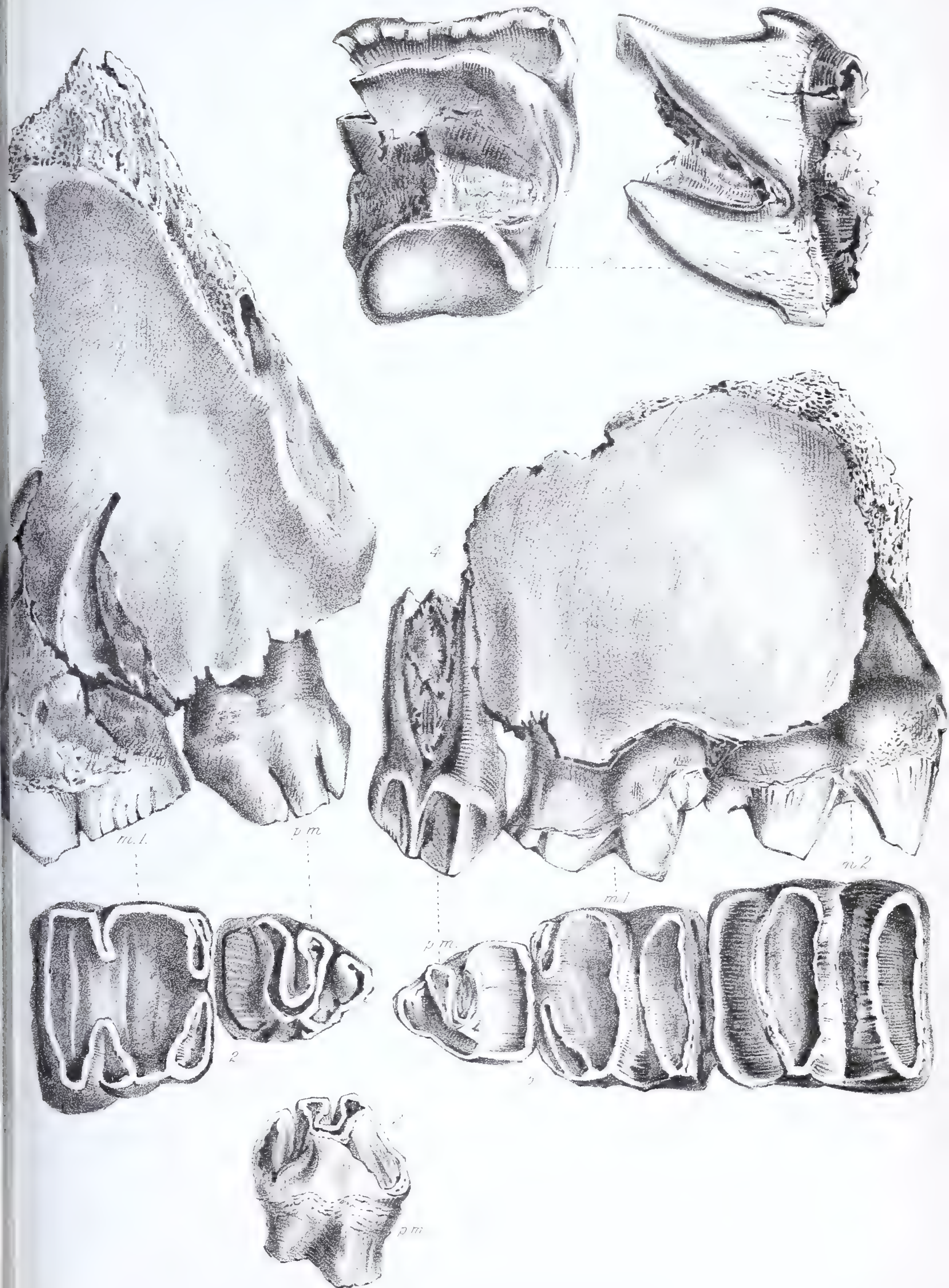

del. lith ad nat

TEETH OF DIPROTODON, QUEENSLAND.

W. West imp.

From these measurements it would appear that No. 2 was about one-fourth smaller than *Diprotodon australis*, and that No. 1 took a place between No. 2 and the latter, but nearer No. 2. The question of the systematic value of the differences between No. 1 and No. 2, on the one hand, and between both of these and *Diprotodon australis*, now arises.

In No. 2, the outer surface of the premolar is ridged, and the crown of the first molar is not so broad as it is long.

In No. 1, the outer surface of the premolar presents simple convexities, without ridges, and the first molar is distinctly broader than long.

In *Diprotodon australis* the form of the premolar is not known; the first molar is somewhat broader than it is long.

I entertain no doubt that Nos. 1 and 2 are specifically distinct; and I propose for No. 2 the name *Diprotodon minor*. Whether No. 1 is specifically distinct from *Diprotodon australis*, or whether its difference in size is merely sexual, I cannot pretend to say, in the absence of any premolar teeth of undoubted *D. australis*.

From the very slight extent to which the premolar is worn while the first molar is so much abraded, I suspect that the former tooth must have persisted for a long while, instead of being pushed out at an early period as in many *Macropodidæ*. In form and pattern the premolar does not depart more widely than the molars themselves from the type found in some Kangaroos, such as *Halmaturus*; and the cast of *Zygomaturus* in the British Museum shows that the upper premolar in that animal had an essentially similar structure, though it seems to have been somewhat larger in proportion to the molars.

DESCRIPTION OF PLATE XXI. [PLATE 38].

Fig. 1. Part of the right upper maxilla of *Diprotodon* (*australis* ?); viewed laterally.
2. The under or oral face of the same fragment.
3. A premolar tooth, apparently from the opposite maxilla of the same animal; viewed from the inner side.
4. Part of the left upper maxilla of *Diprotodon minor*; viewed laterally.
5. The under or oral face of the same specimen.
6. Fourth molar, probably of the same specimen of *Diprotodon minor*.

XXXIII

DESCRIPTION OF A NEW SPECIMEN OF GLYPTODON RECENTLY ACQUIRED BY THE ROYAL COLLEGE OF SURGEONS OF ENGLAND.

Proceedings of the Royal Society of London, vol. xii., pp. 316–326.
(*Read December* 18*th*, 1862.)

In the present brief preliminary notice I propose to give an account of the more remarkable features of the skeleton of a specimen of the extinct genus *Glyptodon*, recently added to the Museum of the Royal College of Surgeons.

The specimen was obtained in 1860, by Signor Maximo Terrero, on the banks of the River Salado, and was presented to the College by that gentleman, through the instrumentality of the late President of the College, J. F. South, Esq.

It arrived in England in an extremely broken and mutilated condition; but by the exercise of great care and patience, Mr. Waterhouse Hawkins, to whom the President and Council of the Royal College of Surgeons entrusted the task of adjusting the scattered fragments, has succeeded in restoring to their natural condition the greater part of the vertebral column, the limbs, and much of the head. In the execution of this laborious undertaking Mr. Hawkins has had, from time to time, all the anatomical aid that Mr. Flower, the Conservator of the College Museum, and I could afford him; and the authorities of the College have finally entrusted me, as one of the Professors of the College, with the duty of describing the specimen.

This duty I propose to discharge by preparing a full description of the skeleton in a memoir to be presented (accompanied by a draught of the requisite illustrations) to the Royal Society. But as

the preparation of such a memoir will require some time, I wish at present to lay before the Royal Society a preliminary account of those particulars in the structure of this animal which must interest anatomists in general as much as the special student of the fossil Edentata, in the hope that the notice may appear in the 'Proceedings' of the Society.

The mass of bony fragments which arrived from South America has afforded material for the reconstruction of the carapace, and of the following parts of the skeleton:—the anterior moiety of the skull with the entire palate; the mandible; some of the cervical, and the greater part of the dorsal, lumbar, sacral and coccygeal vertebræ, with vertebral and sternal ribs; the pelvis and the hind limbs; part of the scapula, and an entire fore limb. And there can be no doubt that all these remains belong to one and the same animal, as no duplicate bones have been discovered, nor any which there is the least reason to believe belong to a different individual. This circumstance gives a particular value to the present specimen, apart from the fact that, notwithstanding the researches of Professor Owen, of D'Alton, of Lund, and of Nodot, our knowledge of the structure of the anterior part of the skull, of the vertebral column and pelvis, and of the fore limb of *Glyptodon* and its immediate allies, is either nil or extremely imperfect. I now proceed to note the more important and the novel anatomical peculiarities which it reveals.

Of the *skull* the new specimen exhibits the anterior moiety, from the anterior boundary of the cranial cavity to the anterior end of the nasal bones, together with the almost entire bones of the face and the lower jaw; it thus furnishes a nearly complete supplement to the fragmentary cranium, consisting of the brain-case and the nasal bones, with the zygomatic processes, formerly described by Professor Owen as a part of *Glyptodon clavipes*, and now set up in the College Museum, together with a carapace, a tail, and a hind foot, as the typical example of that species[1]. In the form of the frontal bone, of the orbits, of the nasal bones, and of the zygomatic process, the skull of the new specimen agrees very closely with that of *Glyptodon clavipes*. From the slighter rugosity of the supraorbital region, the less development of the temporal ridges, and the fact that the nasal

[1] The parts thus combined together were not found so associated, and the question may arise, whether the skull, hind foot, and tail are really parts of the animal to which the carapace (on whose characters the species is founded), belonged. Provisionally I assume that they are. But so many difficulties are involved in the precise determination of the species of these extinct Armadillo-like Edentata, that for the present I leave the question open.

suture persists in the new specimen, I conceive it to have been a younger animal.

The anterior nasal aperture is trapezoidal, and narrower below than above. The vomer is very thick and strong, and the turbinal bones are well developed. The premaxillæ, though small slender bones, enter largely into the lateral boundary of the nasal aperture. Inferiorly they are separated in the middle line by a narrow fissure, which runs back into the crescentic anterior palatine foramen.

The maxillary bones are extremely elongated; while the palatine bones are small in proportion to them, and, like the premaxillæ, are separated by a very narrow median fissure. The extreme length of the roof of the palate, formed by these three pair of bones, is 10 inches; while its width (between the inner edges of the teeth), though rather greater in front than behind, nowhere exceeds $1\frac{3}{4}$ inch. From before backwards the palate has a double curvature, being concave downwards from the anterior end of the premaxilla to the level of the third tooth, and convex thence to the end of the palate-bones; so that the posterior part of the palate has a very marked inclination upwards and backwards.

There were eight teeth in each maxilla, all trilobed, the longitudinal grooves separating the lobes being less marked in the anterior teeth.

The mandible is represented by the two horizontal rami, with the symphysis, the greater part of the right coronoid process, and the entire right condyle, together with many of the sixteen teeth. It very closely resembles the mandibles of *Schistopleuron gemmatum*, described by Nodot, but is wholly unlike the restored jaw of *Glyptodon clavipes* given (on the authority of a drawing) by Professor Owen[1].

The articular surface is situated almost wholly upon the anterior surface of the condyle of the mandible, looking but very slightly upwards; it is transversely elongated, slightly concave from side to side, and convex from above downwards. In all these respects it furnishes a counterpart to the glenoid articular surface of the temporal bone of *Glyptodon clavipes*, already described by Professor Owen.

The length of the head of the present specimen when entire, was probably not less than thirteen inches. The greatest depth of the cranium, from the centre of the frontal bone to the middle of the palate is about 6 inches; the length of the mandible can hardly have been less than 12 inches.

[1] The mandible of the Turin *Glyptodon*, mentioned at the end of this paper, is quite similar to that of the new specimen, and to that of M. Nodot's *Schistopleuron*.

Of the vertebral column, the greater part of the sacral and dorsal region, and some fragments of the cervical region, are preserved. The atter show that the atlas was distinct, but that the axis was anchylosed with one or two succeeding vertebræ, as in the Armadillos The fifth and sixth cervical vertebræ were probably free, but no traces of them have been found. The anterior part of what remains of the rest of the vertebral column consists of a very broad flat bone, composed of three vertebræ firmly anchylosed together, and having their spinous processes represented by a short but very stout osseous knob, which projects upwards and backwards. Anteriorly, these anchylosed vertebræ exhibit on each side of the neural canal an articular facet with a convex surface, resembling a segment of a horizontal cylinder; posteriorly, articular surfaces of a similar character, but concave, are situated in corresponding positions.

Each side of this 'trivertebral bone' presents two large and deep articular cavities for the heads of ribs, fragments of which are still preserved. The anterior rib, remarkable for its stout and massive proportions, was undoubtedly the first; and this circumstance I believe gives a clue to the precise character of the vertebræ which are anchylosed together to form the trivertebral bone; for in the Armadillos the head of the first rib is fitted into a deep fossa, formed partly by the last cervical, and partly by the first dorsal vertebra. Furthermore, the body and transverse processes of the last cervical vertebra in the Armadillos present articular facets of an essentially similar character to those observable on the anterior face of the bone under description[1]; and, finally, the last cervical vertebra is practically immoveable upon the first dorsal in many armadillos, while the two vertebræ are completely anchylosed together in the priodont Armadillo. I conceive, then, that this remarkable bone of the *Glyptodon* is formed by the anchylosis of the last cervical and first and second dorsal vertebræ.

Of the remainder of the spinal column thirteen consecutive vertebræ are preserved; and all of these were immoveably united into one long continuous tunnel or arched tubular bridge of bone, a structure which is without a parallel among the Mammalian Vertebrata. Of these thirteen vertebræ, the four anterior are so completely anchylosed together, that the original lines of demarcation between them are hardly discernible. Persistent sutures separate the fourth from the fifth, and the latter from the sixth; but all trace of the

[1] I may remark in passing, that all the cervical vertebræ of the Armadillos, from the third backwards, are articulated together by joints similar in principle of construction to those which connected together the trivertebral bone of *Glyptodon* with the vertebræ in front of and behind it.

primitive distinction of the sixth and seventh is lost. The other vertebræ are separated by sutures which become coarser and less close posteriorly. In all but the first, second, third, eleventh, and thirteenth vertebræ, the parts representing the vertebral centra are broken away; but where they persist, they are so similar that they were doubtless of similar form throughout. Each centrum is, in fact, a comparatively thin bony plate, so curved as to form a segment of a hollow cylinder of much larger diameter in the front than in the hinder vertebræ, the sides of which pass superiorly into the arches of the vertebræ.

The foremost vertebra of the thirteen is as broad as the posterior part of the 'trivertebral bone,' and presents a couple of convex articular facets which articulate with the lateral articular concavities described above in that bone. The vertebræ rapidly narrow, however, until the fourth is not more than three-fifths as wide as the first, while it is proportionately deeper; and this increase of depth relatively to width goes on until in the thirteenth vertebra the spinal canal is deeper than it is wide.

The spinous processes of these vertebræ are all broken short off; but sufficient remains of their bases to make the following points clear.

The spinous process of the first is almost obsolete, being a mere ridge sloping back towards the second, with which it is continuous. This appears to have been necessary to afford the requisite play for the knob of the trivertebral bone in its movements of flexion and extension on the rest of the spinal column.

The spinous process of the second vertebra was long and thick, and probably somewhat high. It appears to have been completely distinct from the third, which was thinner, and was anchylosed with its successors (as far as that of the twelfth vertebra inclusive) into a long continuous crest. The apices of the spinous processes may, however, have been distinct. So much as is left of the base of this crest shows that it was thickest at the sixth and seventh vertebra (of the thirteen), and that it became thinner both anteriorly and posteriorly.

The spinous process of the twelfth vertebra, forming the termination of the crest, appears to have ended in a free, thin, but rounded edge. What remains of the spinous process of the thirteenth vertebra, on the other hand, thins off anteriorly to a natural edge, which is inclined upwards and backwards. Posteriorly the spinous process becomes very thick and stout, and appears to have had a considerable height. It ends in a fractured hinder margin.

The broad wing-like plates which represent the coalesced transverse processes of the first, second, and third vertebræ of the thirteen, exhibit distinct articular surfaces for the capitula and tubercula of ribs. Further back, the natural edges of the apophysial ridges are broken away, up to the eighth vertebra. Here they are entire on the left side and broken on the right; but, curiously enough, the broken processes are higher than the entire ones, so that the transverse processes in this region of the body must have been asymmetrically developed. The thirteenth vertebra presents peculiarities which could only be made intelligible by a lengthened description, and by figures. The contours of the articular processes become first distinctly traceable at the posterior part of the eleventh vertebra. They are better marked at the posterior part of the twelfth, and at the anterior part of the thirteenth vertebra.

The nervous foramina are not intervertebral, but pierce the arches of the vertebræ throughout the series. In the thirteenth the outlet of the foramen is separated, by a longitudinal bar of bone, into an upper and a lower division.

The posterior part of the thirteenth vertebra is much injured, and does not adjust itself naturally to the anterior end of that part of the lumbar region of the vertebral column (consisting of two vertebræ) which remains continuously anchylosed with the sacrum. One or two vertebræ may possibly be wanting, or even three; but I conceive the last to be the extreme limit of the deficiency[1].

The great Priodont Armadillo has twenty dorsal lumbar vertebræ. If the *Glyptodon* had the same number, there would be three missing; for there are two dorsal vertebræ in the trivertebral plate, thirteen follow it, and two lumbar are anchylosed with the sacral, making altogether seventeen.

The 'sacrum,' composed of anchylosed lumbar, proper sacral, and coccygeal vertebræ, contains at fewest twelve, and perhaps thirteen vertebræ. The centra of the two lumbar vertebræ and of the two proper sacral vertebræ which follow them are preserved. They are thin and broad plates, flat above, and slightly concave below, exhibiting a most marked contrast with the half-cylinder of the hindermost of the thirteen dorsal vertebræ above described. It would seem to require the interposition of at least two, if not three, vertebræ to effect the transition of the one form of centrum into the other.

The last coccygeal is the only vertebra among all those preserved the centrum of which exhibits characters at all like those of an

[1] Unless I greatly err in my interpretation of the photographs, these three missing vertebræ are preserved in the Turin *Glyptodon*.

ordinary mammal, its terminal face being a very broad oval, slightly concave disk. The centrum of the penultimate coccygeal is much flatter and narrower; and this flattening and narrowing predominates still more in the antepenultimate and that vertebra which lies before it, or the fourth from the end. From this point to the two anterior sacrals the floor of the vertebral canal is completely broken away, but there can be no doubt that the centra were represented by a thin bony plate.

The line of the centra of the coccygeal vertebræ forms a very marked arch behind the two sacral vertebræ, whose centra form a nearly horizontal floor; while the dorso-lumbar vertebræ (including the trivertebral bone) form a second arch, flatter than the first.

The spinous processes of all these lumbo-sacro-coccygeal vertebræ, up to the fourth from the end inclusively, are anchylosed together in a long and strong osseous crest, broad and extremely rugose above, eight inches high in front, but slowly diminishing as it follows the curve of the centra posteriorly to five inches.

The spinous process of the penultimate coccygeal vertebra is very thick, but is broken short off. It was probably not less than 4 inches high, and afforded a middle point of support for the carapace between the ischial protuberances. The sides of the median crest, and of the two vertebræ which appear to constitute the true sacrum, are anchylosed firmly with nearly the whole of the inner edge of the vast ilium. Behind these the vertebræ seem to have been devoid of transverse processes, as far as the fourth from the end. But the antepenultimate had a long and slender transverse process on each side; the penultimate has an equally long but much stouter process, while the last coccygeal vertebra has transverse processes of no less length, and extremely stout.

The expanded distal ends of these processes unite with one another and with the inner surfaces of the greatly expanded ischia.

The ilia are immense quadrate bones, slightly concave anteriorly and posteriorly, with their planes so directed as to form rather less than a right angle forwards with the vertebral column. The crest of each iliac bone is thick, expanded, and rugose, and so arched as evidently to have afforded attachment and support to the carapace; which therefore rested directly, partly on the three transversely disposed pillars afforded by the coccygeal vertebræ and the two ischia, partly on the longitudinally arched crests of the sacrum and of the thirteen dorsal or dorso-lumbar vertebræ, and partly on the second great transverse support yielded by the arched crests of the ilia. Apart from their anchylosis, the whole of the parts named

must have been practically fixtures in consequence of this arrangement of the carapace; and the only moveable parts of the vertebral column must have been the tail (of which unfortunately no portion has been found in the present specimen), posteriorly moveable on the last coccygeal vertebra,—the trivertebral bone with its two pair of ribs, capable of an up-and-down motion on the foremost of the thirteen vertebræ,—and then the cervicals, more or less moveable upon the anterior part of the trivertebral bone, and upon one another.

I am not aware of the existence of any mammal in which the vertebral column presents characters of a similar singularity.

The mobility of the rib-bearing trivertebral bone, by a hinge-joint upon the rest of the vertebral column, is peculiarly anomalous. However, if, as appears to have been the case, the heads of the ribs attached to this bone were incapable of movement, and the first rib was furthermore directly anchylosed with the sternum, respiration must have been carried on entirely by the diaphragm, if the anterior dorsal vertebræ had been immoveable on the posterior ones. The hinge-like movement of the trivertebral bone, on the other hand, by permitting the ribs and sternum to describe a longitudinal arc alternately downwards and forwards, and upwards and backwards, would allow of a most efficient bellows action of the thorax, similar in principle to that effected by the ordinary movements of the ribs.

The trivertebral bone is about	6	inches long
The thirteen vertebræ along their convexity...	29½	"
The sacrum..	35½	"
If three lumbar vertebræ are wanting allow...	9	"
	80	

Judging by the analogy of the Armadillos with which the *Glyptodon* presents such close resemblance, and from the shortness of such cervical vertebræ of *Glyptodon* as can be reconstructed, the neck did not exceed in length $\frac{1}{10}$th of the length of the vertebral column from the first dorsal to the last coccygeal. That would give 8 inches for the neck, and would give a grand total for the spinal column, exclusive of the tail, of 88 inches, or 7 feet 4 inches. The length of the carapace of *Glyptodon clavipes* in the Museum of the Royal College of Surgeons is 5 feet 7 inches.

The carpus of *Glyptodon* is in some respects very like that of *Dasypus sexcinctus*, but it consists of eight bones instead of seven, the trapezium and trapezoid being perfectly distinct, instead of forming a single bone, as in *Dasypus*. The scaphoid articulates with the os magnum, and the cuneiform with a metacarpal, as in *Dasypus*.

But it is not a little remarkable that whereas in *Dasypus* it is the fifth metacarpal whose proximal end partially articulates with the cuneiform, in *Glyptodon* the corresponding bone articulated wholly with the cuneiform, and not with any of the distal row of carpal bones. The metacarpal articular end of that bone is, in fact, divided into two facets—an inner, larger, which articulates with part of the proximal end of the fourth metacarpal, and an outer, smaller, which is appropriated by the proximal end of the fifth metacarpal.

That the cuneiform should articulate with two metacarpal bones, and that the unciform should not articulate with the fifth metacarpal at all, are very remarkable peculiarities of the wrist of *Glyptodon*.

The pisiform is a large curved bone, the proximal end of which articulates by a large facet with the ulna, and by a small one with a facet on the palmar aspect of the cuneiform. It closely resembles the same bone in Armadillos.

The trapezium and trapezoid, taken together, have a form closely resembling that of the single trapezio-trapezoid of *Dasypus*. The trapezium possesses only a very small double articular facet on its palmar face. If this gives support to a metacarpal, it must have been very small; and as at present neither it nor any of the hallucal phalanges have been discovered, it is possible the pollex may have been altogether rudimentary. In any case the pollex must have been so much smaller and more slender in proportion than that of *Dasypus*, that the animal must have had a practically tetradactyle fore foot.

The second metacarpal is the longest of all which have been discovered, but is not quite so thick as the third. Its proximal end articulates with the trapezium, trapezoid, and magnum.

The third metacarpal, an almost cuboidal bone, but broader than long, articulates with the magnum, the cuneiform, and the adjacent metacarpals.

The fourth metacarpal, still shorter and broader in proportion, articulates with the unciform and cuneiform, and with the adjacent metacarpals.

The fifth metacarpal has not been found. The two proximal or first and second phalanges are very short, broad, discoidal bones in the second and in the third digits; and the second, which alone exists in the fourth digit, has the same character. The proximal phalanges of the fifth digit have not been found.

The distal or third phalanx is a broad bone, squarely truncated at the extremity, and longer than the rest of the digit, in the second, third, and fourth, and presumably in the fifth digit. Each of these

phalanges is thicker on one side than on the other, so that the upper surface, which is convex from side to side, and also from before backwards, slopes from the thick towards the thin edge.

The distal phalanx of the second digit has its thick edge on its ulnar side, but all the others have their thick edges radial. The distal phalanx of the fifth digit is more pointed, smaller, and thicker in proportion than the others.

The hind foot is quite normal in structure, possessing five toes and the regular number and disposition of tarsal, metatarsal, and phalangeal bones. The third or middle digit is the longest, and its distal phalanx is the longest of all. It is nearly square, and its outer and inner edges are almost equally thick. The distal phalanges of the other toes are all thicker on the side turned towards the middle toe. That of the second toe is almost as square as that of the third ; but the distal angles of that of the third and fourth are bevelled off on the fibular side, while the terminal phalanx of the hallux is similarly bevelled off upon the tibial side. The metatarsal bones have the same thick, prismatic form, and the proximal phalanges the same discoidal character as in the fore foot.

The calcaneal process is directed outwards at an angle of 45° from the axis of the foot, and must have been much raised in the natural position.

While the work of restoration, whose results have just been briefly detailed, was going on, we learned from Dr. Falconer that a nearly entire specimen of a *Glyptodon* was exhibited in the Museum at Turin. An application was at once made to the authorities of the Museum for information, and, if possible, for photographs of this skeleton, and was responded to with the most obliging readiness.

These photographs of a skeleton in some respects more, in others less perfect than that of the College, have confirmed the conclusions already arrived at in the most satisfactory manner ; and I trust before long to be in possession of descriptive details of parts of this specimen which are wanting in our own, and which will enable me to complete the anatomy of the skeleton of the gigantic extinct Armadillo.

XXXIV

LETTER ON THE HUMAN REMAINS FOUND IN THE SHELL-MOUNDS

Transactions of the Ethnological Society of London, vol. ii., 1863, *pp.* 265–266.

JERMYN STREET, *June 28th*, 1862.

MY DEAR SIR,—I regret that the state of my health compels me to leave London before the meeting of the Ethnological Society on Tuesday next, and that, for the same reason, I have been unable to draw up any detailed report upon the human remains submitted to me by the Council.

I regret this the less, however, as the very fragmentary condition of these remains would, under any circumstances, oblige me to speak with very great hesitation in giving an opinion respecting the races of mankind to which they belong.

Although the bones belong to at least four distinct individuals, and there are many portions of skulls among them, there is no cranial fragment sufficiently large to enable me to form even an approximative judgment as to the contour or the capacity of the skull to which it belonged.

Deprived of this most important datum in any ethnological comparison, I have sought for help from the temporal bone, of which there are several, the fragments of upper and lower maxillæ, and part of a frontal bone. The former all exhibit large auditory foramina, well developed mastoid, vaginal, and styloid processes, and well marked supra-mastoid ridges.

The latter prove that the palate was deeply excavated and narrow; that the molars were large and even-sized, forming a series whose inner contour is almost straight; that in the inter-maxillary or incisive part of the upper maxilla, the alveolar margin is remarkably

in advance of the lower edge of the nasal aperture ; in other words, the front contour of the upper jaw sloped downwards and forwards at a low angle, so that the face must have had as prognathous a character as that of an ordinary Australian. Indeed, the left half of an upper maxilla (marked A) corresponds with great exactness with the corresponding part of a bisected skull of an Australian native in the Hunterian Museum.

The teeth in a lower jaw and part of an upper jaw (marked X) are worn down flat, as if by the mastication of hard food.

The fragment of a frontal bone exhibits strong supraciliary ridges, continued across the glabella, and containing well developed frontal sinuses.

That these are very slight materials on which to base any conclusion as to the races to which the remains belonged is obvious enough. But, such as the evidence is, it appears to me to be altogether opposed to the supposition that the bones belonged to either a Malayan race, or to a people allied to the Andaman Islanders. On the contrary, I should be inclined to look among the Papuan races of New Guinea or New Holland for the nearest allies of the men to whom the shell-mound once belonged.

I am, my dear sir, faithfully yours,

T. H. HUXLEY.

DR. HUNT, Secretary of the Ethnological Society.

XXXV

DESCRIPTION OF ANTHRACOSAURUS RUSSELLI, A NEW LABYRINTHODONT FROM THE LANARKSHIRE COAL-FIELD.

Quarterly Journal of the Geological Society of London, vol. xix., 1863, *pp.* 56-68. (*Read December 3rd*, 1862.)

In September last, Mr. James Russell, Mineral Surveyor, of Chapelhall, near Airdrie, called at the Museum of Practical Geology to make some inquiries respecting the probable nature of a fossil (supposed to be a fish) lately brought to light by the workmen engaged upon the Monkland Iron and Steel Company's estate, about a mile from Airdrie and twelve miles east of Glasgow, and found in what is known as the Airdrie or Mushet's black-band Ironstone.[1] I was at that time absent from London; but Mr. Etheridge, to whom Mr. Russell described the fossil, strongly advised that a careful drawing should be made and sent up to London, for my examination. This was eventually done, and the sketch, faithfully executed in its general characters, which reached me on the 6th of November, appeared so conclusively to indicate the Labyrinthodont nature of the fossil, that I at once requested Mr. Russell to permit me to have it sent up to the Museum for closer examination. Mr. Russell very

[1] The President has kindly furnished me with the following note respecting the stratigraphical position of the Airdrie black-band Ironstone:—

"The fossils described in this memoir were found in, or else close to the 'Airdrie or Mushet's black-band' Ironstone, which at this point changes into Coal. According to Mr. Ralph Moore's published section, this stratum lies about 564 feet below the topmost Coal-measures, and about 666 feet above the 'Moorstone rock,' which I believe to be the general equivalent of the English Millstone grit. The bones were therefore found in the true Coal-measures, far above the Gilmerton Limestone series (the equivalent of part of the English Carboniferous limestone, in which *Loxomma* was discovered), and probably 2000 feet or more above the horizon of the Burdie House limestone."

obligingly consented to this proposition, and the specimen reached me in perfect safety on the 27th of November, my interest in it having in the meanwhile been greatly heightened by the reports respecting its characters which had reached me from Professor Rogers, Mr. David Page, and Mr. Armstrong of Glasgow.

A glance at the fossil was sufficient to satisfy me that these reports had not unduly exaggerated its merits. It exhibited, in fact, the greater part of the contour of a skull, 15 inches long by 12 inches wide at the widest part. That the under or palatine surface of the skull was turned towards the eye was obvious from the numerous stumps of broken teeth which followed the anterior moiety of its contour ; but almost the whole of this surface was obscured by a thick coat of the matrix, in which were partially imbedded many of the long and pointed crowns of the teeth. These had been broken off, and lay not very distant from their stumps, with their points all directed inwards, towards the middle line of the palate. Their arrangement was just such as might have been expected if the axes of the teeth had naturally been turned somewhat inwards, and the vertical crush of the superincumbent strata, after the fossilization of the skull, had consequently caused them all to fall inwards as they broke. The same pressure has produced a slight asymmetry of the whole skull.

From the proportional size and structural features of the teeth, and from the general contour of the skull, I concluded this to be a new genus of Labyrinthodonts ; but in order to make sure of the point, I proceeded to develop the fossil, from the hard matrix in which it was imbedded, with much care ; removing some of the teeth and, on one side, even a portion of the bony palate, in order to obtain a view of those parts, such as the orbits and posterior nares, which would enable me to decide the question.

The skull, as it now appears (fig. 1), presents almost the whole of its palatine or inferior surface to view, with the exception of the right temporal region. Its greatest length, measured along a median line drawn from the middle of the premaxillary region to a level with the posterior and external points of its prolonged and broad temporal prolongations, is 15 inches. Its greatest width, obtained by doubling the distance from the left posterior and outer margin to the middle line, is 12 inches. Opposite the great vomerine tusks (*d*), the skull measures 5·3 inches in width. It diminishes slightly from this point to the rounded snout, and gradually increases in breadth posteriorly to the level of the supratemporal foramina (*c*), where it measures about 10 inches in width. Beyond this point it widens suddenly by

about half an inch on each side, and the lateral contours continue to diverge from hence to a point about $2\frac{1}{2}$ inches distant from the hinder extremity of the temporal prolongations of the skull. The external contour of the temporal prolongation now becomes rounded off, and sweeps evenly inwards, until it meets the internal contour, which appears to be nearly straight. The epiotic processes are not visible.

In the middle line of the base of the skull, extending as far backward as the level of the posterior part of the supratemporal foramen, is the well-ossified basisphenoid, 1·7 inch broad, and slightly excavated posteriorly. The basisphenoid narrows anteriorly, so that, at 1·4 inch from its posterior extremity, it is not more than 0·9 inch wide; beyond this point it suddenly widens to form the lateral processes, like those commonly exhibited by the basisphenoid of fishes, and then rapidly tapers forward, having, at 2·8 inches from its hinder extremity, a diameter of not more than 0·25 inch, and continuing straight and style-like as far as it can be traced, which is to a distance of about 6 inches from its hinder extremity.

The limits of the vomers cannot be accurately defined; but they are very broad plates, separating the large anterior palatine foramina (*a*) from the comparatively small posterior nares (*b*), which are round apertures, 1 inch in diameter, and 5 inches from the anterior end of the snout, situated between the vomer, the maxilla, and the palatine bones on each side. The vomers unite in the middle line with one another and with the prolonged anterior extremity of the basisphenoid. Posteriorly they are connected with the palato-pterygoid arcade, the separate components of which cannot be accurately defined. The palatine portion, however, is a broad, flat plate, measuring 3·5 inches between the posterior nares and the palato-temporal foramen. It is united externally with the maxilla. Internally it is separated by a narrow interval from the basisphenoid. Posteriorly it passes into the pterygoid portion, which is narrow and curves outward, beneath the inner contour of the temporal prolongation of the skull, to be lost about the posterior and internal angle of that region. Externally the margin of the pterygoid portion is arcuated, to form the boundary of the palato-temporal foramen. Through this foramen the under surface of the upper wall of the skull in the temporal region becomes visible. The sutures separating the component bones of this region are not visible; but on the level of the posterior end of the basisphenoid it presents an elongated aperture, or supratemporal foramen (*c*), 1·3 inch long by 0·4 inch wide. The long axis of this foramen is directed obliquely forwards and inwards, and it is nearer the pterygoid than the external boundary of the palato-temporal foramen.

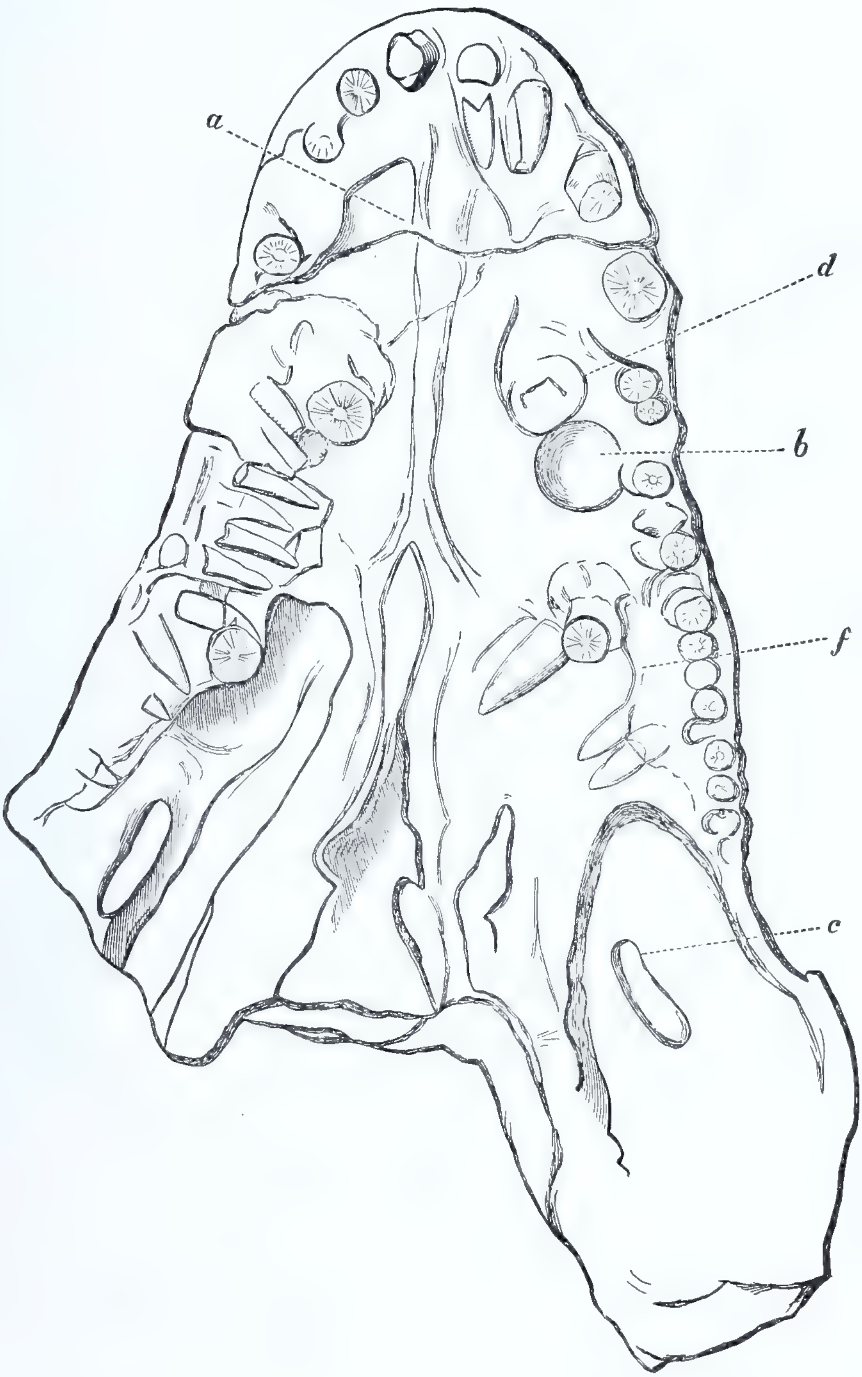

Fig. 1.—*Palatine aspect of the skull of* Anthracosaurus Russelli.

(One-third of the natural size.)

a. Anterior palatine foramen. *b*. Posterior nares. *c*. Supratemporal foramen. *d*. Place of attachment of left vomerine tusk. *e*. Vomerine tooth. *f*. Palatine teeth and alveolar plate.

Although I worked out this region of the skull with extreme care, I was in doubt whether the aperture in question was really a natural one, until I cleared away the matrix from the opposite side, and there found a foramen of quite a similar character, though distorted by the crushing of this part of the skull.

The premaxillary bones, strong and arched, send back two processes from their opposed ends, which run upwards and backwards in the middle line (in the manner common in Amphibia) towards the junction of the vomers. As the anterior portion of the vomerine plate is inclined upwards and forwards, it follows that the most anterior region of the palate has a somewhat arched roof, as in the Frog. The anterior palatine foramina (*a*), included between the recurrent processes of the premaxillaries, their dentigerous processes, and the vomers, appear to be about $1\frac{1}{2}$ inch long by 1 inch wide; but it is difficult, from the condition of the fossil, to define their limits with exactitude.

Thirty-seven teeth, or remains of teeth, are visible. Of these, on the left side, thirteen are situated in the premaxilla and maxilla, and three on the palatine bone; while, on the right side, nineteen are attached to the premaxilla and maxilla, one to the vomer, and one to the palatine bone. On the whole, the maxillary teeth decrease in size from before backwards, but not very regularly. The first tooth on the left side was 1·7 inch long when entire, by about half an inch thick at the base. The second immediately follows it, and is somewhat larger. The third, of about the same size as the second, is separated from the latter and from the fourth, by spaces about three-quarters of an inch wide. The fourth tooth, broken short off, must have been a very large one, being not less than three-fourths of an inch in diameter at the base. It is separated by a deepish fossa, 0·7 inch wide, from the succeeding tooth. This, the fifth, is close to the sixth, and both are small, the base of neither attaining more than 0·3 inch in diameter. The seventh and eighth teeth, rather large, are situated at tolerably equal intervals from one another, and from their predecessors and successors, in the interspace of about 2 inches which separates the sixth from the ninth tooth. There are marked fossæ, as if for the reception of the points of mandibular teeth, between them. The bases of the ninth and tenth teeth, close together, occupy 0·7 inch. They are separated by a space of about half an inch from the eleventh tooth, and this by a somewhat smaller interval from the twelfth, which is close to the thirteenth. The bases of these last-mentioned teeth do not exceed 0·4 inch in diameter. The last tooth is nearly on a level with the anterior margin of the palato-temporal foramen. There is a fossa of nearly the same size

as its base behind it, but no trace of the attachment of any other tooth.

The premaxillary and maxillary teeth on the right side by no means exactly correspond, either in position or in size, with those on the left.

The tooth nearest the middle line in the right premaxilla is six-tenths of an inch in diameter, and its base and its several fragments, when put together, show that it had a length of at least an inch and three-quarters. The two succeeding teeth are about half an inch in diameter at the base, and are not more than a quarter of an inch apart. Then follows an interspace of 0·9 inch, in which I think I can trace the remains of the attachment of a great tusk. Then comes a large tooth, 0·7 inch in diameter at the base; and then four small ones, none of which exceed 0·3 inch. The crowns of the succeeding teeth are all broken off, and lie with their points inwards upon the matrix, which covers this region and obscures their broken roots. None of them, however, have a basal diameter of more than 0·35 inch, and the last measures hardly more than 0·2 inch at the base. The anterior of these teeth are about 1·3 inch in length, while the hinder ones become shorter, until the last was probably not more than half an inch long when entire. The right vomer gives attachment to an immense tusk, 0·8 inch in diameter at the base. It could hardly have been much less than three inches long, but it is unfortunately broken short off. The left vomer presents the surface for the attachment of a similar tusk, but the tooth itself is entirely detached. There is not the least trace of the existence of any other vomerine teeth besides these.

On the left side, the palatine bone, eight-tenths of an inch behind the posterior nasal aperture, supports a tusk 0·6 inch wide at the base, which, when entire, was very nearly 2 inches long. The palatine bone is raised up into a ridge, so as to form a sort of alveolar wall on the outer side of this tusk, and the wall is continued backwards as a thin plate of bone directed almost horizontally inwards (*f*). At a distance of three-quarters of an inch from the great anterior tusk, the alveolar plate, the margin of which is excavated in the interval, affords support to a tooth 0·35 inch in diameter at its base, and this is immediately followed by another of the same dimensions. These teeth are about 0·9 inch long.

On the right side, the base of a similar palatine tusk and part of an alveolar plate are visible; but there are no small teeth, and the tusk is situated nearly an inch further back than on the left side. But the alveolar plate extends forward in front of this tusk, and presents a deep sinus, in which I suppose a tusk corresponding to that on the

opposite side may have been developed. If the sinus upon the palatine alveolar plate of the opposite side has the same signification, it would appear as if there were normally two great palatine tusks on each side, but that the anterior and posterior of opposite sides are shed simultaneously.

The fossil was broken into two pieces when it reached me; the fracture passing obliquely between the third and fourth teeth on the left side, and through the fourth on the right. The fractured surface shows the roof of the skull, or rather the snout, and proves that it was raised into a broad longitudinal ridge, so convex as to be almost semicircular, about 1·5 inch broad and 0·6 inch above the general level of the facial bones. From the sides of this convexity, the sides of the face slope with a gradual curve towards the alveolar margin. The depth of the skull, immediately over the centre of the maxillary alveoli, is rather less than one inch. From the centre of a line joining the margins of the alveoli to the top of the central ridge is a distance of about 1·9 inch; and in the occipital region the skull is not deeper: considering its breadth and length, therefore, the skull is extremely flat.

The teeth are round, or slightly oval in section at their bases, and throughout the greater part of their length. They taper gradually to sharp points and become slightly incurved towards their apices. Their bases are not grooved, but, on the contrary, are marked by numerous delicate and sharp longitudinal ridges, so that transverse sections appear to be very slightly polygonal. Towards the apex of the tooth, two of these ridges, an anterior and a posterior, become more distinctly marked, and, combined with a very slight flattening of the tooth, give it a double edge.

In one of the anterior teeth, the front face towards the point is much worn, as if by attrition against one of the mandibular teeth.

Transparent transverse sections of the teeth exhibit a singularly beautiful and complex structure. The relatively small pulp-cavity sends off primary radiating prolongations, which pass straight to the circumference of the tooth, and at a small distance from it terminate by dividing, usually, into two short branches, each of which gives off from its extremity a wedge-shaped pencil of coarse dentinal tubuli. These spread out from one another, and terminate in a structureless or granular layer, which forms the peripheral portion of the dentine, and, from the small irregular cavities scattered here and there through its substance, reminds one of the 'globular dentine' of the human tooth. An extension of this peripheral layer is continued towards the centre of the tooth, between every pair of primary prolongations

of the pulp-cavity. The short secondary processes which are sent out from opposite sides of the primary prolongations of the pulp-cavity, give off in the same way, from their ends, pencils of conspicuous dentinal tubuli, the ends of which terminate in the inward extensions of the peripheral layer. The secondary processes of adjacent primary prolongations alternate and, as it were, interlock with one another, so that the inward extension of the peripheral layer takes a sinuous course between them. A thin layer of dense and glassy enamel invests the tooth continuously, but sends no processes into its interior ; and, of course, under these circumstances there can be no cement in the interior of the tooth, nor can its surface be said to be plaited or folded. It will be understood that this description gives merely the principle of arrangement of the parts of the tooth : its details could only be made intelligible by elaborate figures.

In *Rhizodus* and in *Ichthyosaurus* the principle of construction of the complex tooth is totally different, the surface of the tooth being really folded, and prolongations of the cement being continued into the folds.

Addendum, January 14, 1863.

The Referee, to whom the preceding description of the skull of *Anthracosaurus* was sent, has suggested that it is desirable I should express some opinion respecting the systematic relations and affinities of the fossil. I am glad that I am in a far better position to comply with this suggestion now, than I was when the description of the cranium was sent to the Society ; for at that time I was not in possession of the valuable evidence regarding the characters of the vertebral column, which has come into my hands within the last few days through the exertions of my indefatigable correspondent, Mr. Russell.

For some years past, I have been acquainted with well-ossified vertebræ and ribs from the Carboniferous formation ; but the vertebræ have always been devoid of their arches and processes ; and though the ribs presented characters suggestive of their belonging to a higher division of the Vertebrata than Fishes, I thought it better to wait for further evidence as to their real nature before giving any account of them.

More than a year ago, I brought away with me from the collection of the Earl of Enniskillen, at Florence Court, a remarkable rib and vertebral centrum. I have seen similar remains in the admirable collection of Dr. Rankin, of Carluke ; and, more recently, Mr. Russell has sent me up a number of vertebral bodies of different kinds from

the Airdrie workings. I had every reason to believe some of these vertebræ to belong to *Anthracosaurus*, and it was with that conviction in my mind that I ventured to caution the members of the Geological Society, on the occasion of the reading of Mr. Marsh's paper on "*Eosaurus Acadianus*,"[1] against too hastily concluding that the vertebral centra, which he had found in the Nova-Scotian coalfield and then described, were necessarily Ichthyosaurian,—seeing that I had much reason to suspect that they might belong either to Labyrinthodonts or to some genus of intermediate characters, between Labyrinthodonts and Ichthyosaurians.

Within the last few days Mr. Russell has sent me the vertebra of which an outline view is given in fig. 2 (one-half the natural size). It

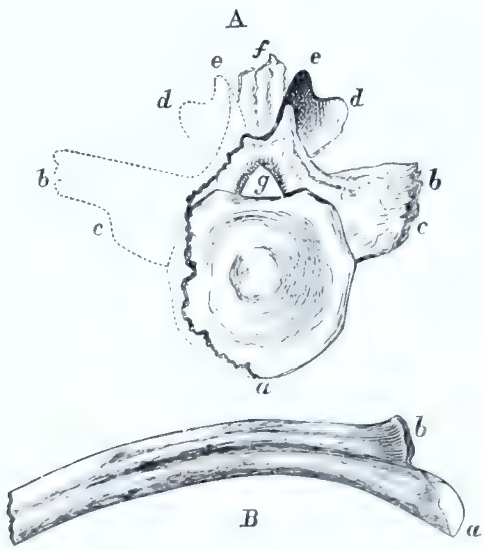

Fig. 2.—A. *Dorsal vertebra of* Anthracosaurus, *viewed from behind.* B. *Rib of the same Amphibian.*

A.—*a.* Body of the vertebra. *b.* The longer division of the transverse process, and *c.* The shorter division. *d.* Anterior zygapophysis. *e.* Posterior zygapophysis. *f.* Spinous process. *g.* Neural canal. B.—*a.* Capitulum. *b.* Tuberculum.

was found in the same bed as that which yielded the skull of *Anthracosaurus*, and corresponds very well in size with what one might expect would be the dimensions of a dorsal vertebra of that animal. Associated with it on the same slab are several other less complete vertebræ and the remains of two ribs.

The body of the vertebra is greatly flattened from before backwards, as the subjoined measurements will show. The exposed articular surface is concave, and a section which I have had made of

[1] See Quart. Journ. Geol. Soc., vol. xix, 1863, p. 52.

a similar vertebral body shows that it was equally concave upon both sides. The concavity, however, is not conical in section like that of a fish's vertebra, but its sides are a little convex, rising slightly, within the margin. Hence the section of this vertebra has very much the same appearance as that of Mr. Marsh's problematical vertebra represented in the figure which accompanies his paper.[1]

The contour of the vertebral body is not circular, but is slightly angulated, so that it would tend to be octagonal were not the place of the uppermost angle of the octagon occupied by the excavated floor of the neural canal. The short sides of the vertebral body are concave from before backwards, and in other specimens exhibit a slightly rugose marking.

The neural arch is very small in proportion to the size of the body of the vertebra, and its contour is nearly that of an equilateral triangle with a curved base.

The very stout sides of the neural arch are continued upwards into a strong spinous process, which is broken off a short distance above its origin and nearly on a level with the upper parts of the zygapophyses. Of the latter the posterior pair are turned towards the eye, and are much broken. The hinder face of the right anterior zygapophysis is visible (at *d*), and its curved contour is nearly entire.

The transverse process of the right side (the only one preserved) springs by a long line of origin from the lower part of the neural arch and from the upper half of the circumference of the vertebral body. It is greatly flattened from before backwards, and its lower half (*c*) ends, at a distance nearly equal to half the diameter of the body of the vertebra, in a rounded edge, which appears to be complete and unbroken. The upper half, on the other hand, terminates in an obviously rough and fractured extremity. I conclude from this circumstance, and from the characters exhibited by the proximal ends of the ribs, which I shall immediately describe, that the upper division of the transverse process extended much further outward than the lower, and I have indicated this in the dotted restoration of the left side of the vertebra.

	inch.
Height of body of vertebra	1·6
Transverse diameter	1·6
Length	0·47
Height of neural arch	0·3
Depth of transverse process	0·8
Thickness of transverse process	0·2

[1] Am. Journ. Science, n.s., vol. xxxiv. pl. 2. fig. 2.

The best-preserved rib is 6½ inches long[1] and half an inch broad, measured in a direction perpendicular to its length. It is, however, much flattened from before backwards, so that its thickness does not amount to more than one-sixth of an inch. The face of the rib is not flat, but it is somewhat excavated, so that the bone is thinner in the middle than at the edges. At its proximal end the rib exhibits a very distinct *tuberculum* and *capitulum*. The former projects, so as to disturb the sweep of the curve of the convex side of the rib and to convert it for a short distance into a concavity, and it is abruptly truncated posteriorly. The capitulum of the rib continues the line of its general curvature for half an inch beyond the tuberculum, and ends in a rounded extremity. I presume that the capitulum articulated with the lower half of the transverse process (*c*), and that the tuberculum articulated with its upper half, in which case the distance (*a*, *b*) on the rib would be practically equal to the excess of length of the upper division of the transverse process over that of the lower.

The skull, a dorsal vertebra, and a rib of *Anthracosaurus* being known, I now return to the question, what are the affinities of that Labyrinthodont?

The large size of the teeth, the comparative solidity of their bases, and the complex character of the labyrinthic ramifications of the pulp-cavity are all characters in which *Anthracosaurus* resembles the *Mastodonsaurus* of von Meyer and Plieninger and its allies, and differs from *Archegosaurus*. Whether *Anthracosaurus* had well-ossified occipital condyles like *Mastodonsaurus*, or cartilaginous ones such as were probably possessed by *Archegosaurus*, does not appear, the fossil being defective in this region. In the large size of the anterior palatine foramina, the extent to which the palate-bones are united with the maxillaries, in the form of the pterygoidean arch and that of the basisphenoid, *Anthracosaurus* is nearer to *Archegosaurus* and *Dasyceps* than to *Mastydonsaurus*.

But the vertebræ are altogether Mastodonsaurian. The vertebræ of *Mastodonsaurus* were described and figured in 1844 in the well-known work of von Meyer and Plieninger, 'Beiträge zur Paläontologie Wurtembergs.' No fewer than seventeen vertebræ were discovered in one slab, together with the skull of this remarkable Labyrinthodont; another block contained eight vertebræ, belonging to the same animal, but not immediately succeeding the former; and a third slab of stone

[1] The sternal end of the rib is broken off. It was certainly much longer when perfect, as the rib from Lord Enniskillen's collection, though more slender, measures 8½ inches along its curve, and still presents a fractured extremity.

contained five more trunk-vertebræ, besides three others which were caudal. Dr. Plieninger seems inclined to think that all these cervico-dorsal vertebræ belonged to one animal: but even the fact that seventeen vertebræ were found together in one block, and the existence of caudal vertebræ, must be amply sufficient to satisfy every anatomist of the untenability of the hypothesis that the Labyrinthodonts were frog-like or toad-like in form.

The trunk-vertebræ of *Mastodonsaurus* are biconcave, and much flattened from before backwards. The neural arch ends above in a strong spinous process; there are well-developed zygapophyses, and the stout transverse processes exhibit a division into an upper longer and a lower shorter portion. So far they are very similar to those of *Anthracosaurus*. The ribs again are strikingly similar to those of *Anthracosaurus*, as may be seen by comparing plate 5, figs. 1 & 2 of the work cited with fig. 2, B.

On the other hand, the vertebræ of *Mastodonsaurus*, according to Plieninger, presented characters which I do not meet with in *Anthracosaurus*. Thus, the articular surfaces of the bodies of the vertebræ of the Triassic Amphibian are inclined towards one another superiorly, while those of *Anthracosaurus* are parallel; and the upper and lower portions of the transverse process, which are said by Plieninger to be separated by a suture, so that the neural arch, with the upper longer transverse processes, readily separates itself from the body with the lower and shorter transverse processes, are, so far as I can observe, perfectly continuous in the Carboniferous Amphibian.

Double transverse processes, the upper more particularly connected with the neural arch, and the lower with the body of the vertebra, are to be found, though the circumstance does not seem to have received much notice from palæontologists, in several genera of *Saurobatrachia*, or Salamandroid Amphibians.

In *Salamandra maculosa*, for example, each cervico-dorsal vertebra, except the atlas, has, on each rib, a prominent transverse process inclined backwards; and all these processes, except perhaps the very last, are deeply bifid, so as to be divided down nearly to their origin into two more or less divergent processes. The upper division comes off distinctly from the neural arch, while the lower arises for the most part below the level of the upper margin of the articular face of the body of the vertebra. The transverse processes of the three or four anterior caudal vertebræ are also bifurcated at their ends, and at the eighth or ninth caudal the transverse processes cease to be distinguishable.

The proximal ends of the four anterior pairs of ribs are divided

into capitular and tubercular processes of nearly equal length, and possess a distinct 'angle,' whence a process is given off upwards and outwards.[1] In the hinder ribs the tuberculum becomes a little shorter and more slender than the capitulum. In *Pleurodeles Waltlii*, the vertebral column and the proximal ends of the ribs resemble those of *Salamandra maculosa*, though the division of the transverse processes is less marked, and the capitulum and the tuberculum of the ribs are not so deeply separated; indeed, posteriorly, the separating cleft becomes almost obsolete. In *Euproctes* the division of the transverse processes is hardly discernible; nevertheless there is a rudiment of the angular processes in the anterior ribs. In other *Saurobatrachia*, a groove on each side, indicating an incipient division of the proximal end of the rib, is not uncommon. In all these cases I am not aware that the single or bifid character of the transverse processes is correlated with any notable differences in other parts of the organization.

It appears to me, then, that the characters of the certainly Labyrinthodont vertebræ[2] made known by von Meyer and Plieninger, and in the present paper, are in perfect accordance with the view originally put forward by Professor Owen, that these animals are more closely allied to the *Batrachia* than to any of the *Reptilia* proper. But I conceive that the affinities of the Labyrinthodonts are clearly with the *Saurobatrachia* (and, in some cranial characters, with the *Cæciliæ*), and not with the *Anura* as was at first suggested; and, with every deference to the opinion of so great an authority on all that relates to the Labyrinthodonts as von Meyer, I must venture to doubt whether, in any characters, these *Amphibia* exhibit a real approximation to the *Reptilia*.

At present we are acquainted with two apparently very distinct types among the Labyrinthodonts—that of the ARCHEGOSAURIA (*Archegosaurus*), at present known to occur only in the Carboniferous rocks, and that of the MASTODONSAURIA (*Mastodonsaurus*, *Labyrinthodon*, *Capitosaurus*, *Trematosaurus*), which seem to have flourished in remarkable abundance during the Triassic epoch. Both groups exhibit the sculptured and polished[3] surface of the crania, the vomerine and palatine teeth, the forwardly situated posterior nares, the

[1] Plieninger notes what appears to be a process of a similar character to this in the ribs of *Mastodonsaurus*.

[2] It does not appear that there is any evidence to show that the vertebræ ascribed to *Labyrinthodon* by Professor Owen in his paper on the Warwickshire Labyrinthodons (Geol. Trans. 1841) are such, while there is much reason to believe they are not.

[3] Whence the term 'Ganocephala' as a distinctive appellation of the *Archegosauria* is inadmissible.

permanently distinct epiotic bones, the divided supra-occipital, the three sculptured pectoral plates, the elongated, caudate, salamandroid body, and the comparatively short limbs and weak feet which are distinctive features of the Labyrinthodont *Amphibia*, as well as the more or less complex ramifications of the pulp-cavities of the teeth, which they share with Fishes and *Ichthyosauria*.

But the *Archegosauria* have imperfectly ossified vertebral bodies,[1] while the *Mastodonsauria* have them thoroughly well ossified, though still biconcave; and the *Mastodonsauria* have double ossified occipital condyles, which have not been found in *Archegosauria*.

Of the other distinctions, if such there were, of the two groups, we know very little. It is true that the *Archegosauria* had, as von Meyer has proved, in his splendid monograph 'Die Reptilien des Stienkohls,' a persistent branchial apparatus and a very remarkable scaly ventral armature. But what do we know with certainty about the presence or absence of corresponding structures in the Triassic *Mastodonsauria?* Whatever may be the nature of the doubtful *Anisopus* or *Rhombopholis*, it is certain that the African, probably Triassic, *Micropholis* was protected by ventral scutes; and until Mastodonsaurian Labyrinthodonts are found preserved as favourably as the *Archegosauria* have been, I think it will be hazardous to take it for granted that they had neither ventral scutes nor even persistent branchial arches.

If we adopt these two divisions and endeavour to range the known Carboniferous Labyrinthodonts under one or the other,—*Archegosaurus*, of course, takes its place among the *Archegosauria*; and *Pholidogaster*,[2] I suspect, must go with it, though its vertebræ are far better ossified, and the condition of the cranial condyles is not known. *Baphetes* and *Parabatrachus* are too little known to justify us in arriving at any conclusion respecting them; and the like is true of *Loxomma*. As regards the *Raniceps* of Wyman (Am. Journ. of Sci. and Arts, 1858), the *Dendrerpeton* and *Hylonomus* recently discovered by Dr. Dawson in the Nova-Scotian coal-field, and the new genus *Hylerpeton* instituted by Professor Owen, from the same locality, I do not think we are even in a position to say that they are Labyrinthodont, much less whether they have Archegosaurian or Mastodonsaurian affinities. Among the many remains discovered by the zealous research of Dr. Dawson, I do not know that a single specimen of one

[1] It seems to me probable that the vertebral centra of *Archegosaurus* may really have been osseous rings, such as are found in embryo frogs and salamanders, and as persisted in *Megalichthys* and probably in *Rhizodus*, and that they have broken into the separate pieces described by von Meyer in the process of fossilization.

[2] Quart. Journ. Geol. Soc. 1862.

of the pectoral plates, so characteristic of all Labyrinthodonts, has made its appearance. They may possibly have been *Amphibia*; but their skulls, their cycloid scales, and their deeply biconcave, fish-like, vertebral centra appear to me to indicate a closer affinity with the *Ophiomorpha* (*Cæcilia*, *Ichthyophis*, &c.) than with the *Labyrinthodontia*.

Of the unquestionable Labyrinthodonts which occur in the Carboniferous rocks, then, *Anthracosaurus* is the only genus regarding the vertebral column and ribs of which there is any information; and the description and comparisons which I have given seem to me to necessitate the conclusion that, side by side with the Archegosaurian type, the Mastodonsaurian type of vertebral organization, hitherto known to occur only in the Trias,[1] was well developed in the *Anthracosaurus* of the Scotch coal-field. At the same time, the anchylosed condition of the neural arches, the supratemporal foramina (which may, however, be parts of the 'mucous grooves' common upon Labyrinthodont skulls, the floor of which was very thin, or merely membranous in the temporal region of *Anthracosaurus*), and the strong median convexity of the snout, separate *Anthracosaurus* from any known Triassic Labyrinthodont. And though, in the general form of the cranium and in some other respects, *Anthracosaurus* has a certain resemblance to the Permian *Dasyceps*, it differs as widely as possible from it in its dentition.

[1] Nothing is at present known of the vertebræ of *Dasyceps Bucklandi*, from the Bunter sandstein of this country. See Memoirs of the Geological Survey of Great Britain:—The Geology of the Warwickshire Coal-field; by H. H. Howell, F.G.S. 1859.

XXXVI

FURTHER REMARKS UPON THE HUMAN REMAINS FROM THE NEANDERTHAL.

The Natural History Review, 1864, *pp.* 429–446.

SINCE the remarkable skull, discovered in a cave of the valley of the Düssel was introduced to the special notice of the English scientific world in the pages of this Journal,[1] it has become the subject of many discussions, and even of not a few special commentaries, for one or two of which I am myself responsible. Partly on this ground, partly by reason of the inherent interest of the subject, I propose now to give some account of, and to remark upon, the four essays on the Neanderthal skull which appear to me to be of most importance; viz. that by Professor King,[2] that by Professor Mayer,[3] that by Professor Schaafhausen,[4] and that by Mr. Turner.[5]

1. Professor King considers the differences between the Neanderthal skull and all other human crania to be so considerable, that he is not only quite certain of its belonging to at least a distinct species—*Homo Neanderthalensis*—but, at the end of his communication, even feels "strongly inclined to believe that it is not only specifically but generically distinct from Man," considering that he has satisfactorily shown "that not only in its general but equally so in its particular characters, has the fossil under consideration the closest

[1] Natural History Review, 1861.

[2] The reputed fossil man of the Neanderthal. The Quarterly Journal of Science. No. 1. Jan. 1864.

[3] Ueber die fossilen Ueberreste eines Menschlichen Schädels und Skeletes in einer Felsenhöhle des Düssel—oder Neander-thales. Müller's Archiv. 1864, No. 1.

[4] Sur le crâne de Neanderthal. Bull. de la Société d'Anthropologie, 1863–1864.

[5] The Fossil Skull Controversy. On human crania allied in anatomical characters to the Engis and Neanderthal skulls. The Quarterly Journal of Science. No. 2, April, 1864.

affinity to the apes. Only a few points of proximate resemblance have been made out between it and the human skull, and these are strictly peculiar to the latter in the fœtal state."

The whole purport of my essay on this subject,[1] having been to prove a proposition exactly opposite to Professor King's, viz. that among recent human skulls it is possible to select a series which shall lead by insensible gradations from the Neanderthal skull up to the most ordinary forms, I must refer to the arguments used therein, contenting myself with assuring Professor King that I have not in the slightest degree, "assumed a resemblance closer than exists" between certain Australian crania, and the Neanderthal skull; on the contrary, I shall endeavour to show by additional evidence at the end of the present notice, that a cast of the interior of the skull, representing the brain of the Neanderthal man, presents an even closer resemblance in form to a cast of the interior of a particular Australian skull than does the exterior of his skull.

2. Professor King, as we have just seen, regards the Neanderthal man as a new species at least, perhaps as the type of a new genus. Geheime-Rath Professor Mayer of Bonn goes to the other end of the scale of opinion, and propounds the hypothesis that the debateable skull was, after all, only that of a rickety "Mongolian Cossack," belonging to one of the hordes driven by Russia, through Germany, into France in 1814.

I had written that Professor Mayer *gravely* propounds this hypothesis, but I have erased the italicised word; for, in truth, the work is not gravely done, but is laden with numerous jocosities of small size, but great ponderosity, directed against Mr. Darwin and his doctrines. Such recalcitrations will not greatly affect that sick lion, but it must be confessed they do not lead one to feel much tenderness towards his assailant. And yet, as I shall proceed to show, the learned Professor can hardly afford to throw stones with so much vehemence and so little discrimination.

The opening passage of his essay, for example, contains as many errors as paragraphs.

"The discovery of these fossil fragments of a human skeleton, or rather of a skull only, has lately excited so much attention among the naturalists of England, and they have based such far-reaching conclusions [weitgreifende Folgerungen] upon it, although acquainted with nothing more than the figure of the calvaria on a small scale, given by Professor Schaafhausen in Müller's Archiv for 1858 (1), that I am instigated to publish my own investigations on these fossil

[1] Evidence as to Man's Place in Nature, 1863.

remains, which their possessor, Professor Fuhlrott of Elberfeld, permitted me to examine soon after their discovery.

"Professsor Huxley namely affirms that the fossil skull of the cave in the valley of the Düssel, is, among all skulls, admittedly belonging to an epoch anterior[1] to the present, the most ape-like (2). Along with and in demonstration of this proposition, he speaks of a short sagittal suture, which, however, is no longer present, either externally or internally, and considering the dolichocephalic form of the skull must at a previous period certainly have been long(3); and further of a want of space for the posterior lobes of the cerebrum, although the calvaria exhibits a not inconsiderable arching of the upper part of the squama occipitis.(4) According to this, a homo pithecöides formerly dwelt in this rock cavern (known as the lesser "Feldhofgrotte") as a Troglodytes (5)! ?

"But I leave these conclusions aside, &c."—pp. 1 and 2.

I propose to comment upon the passages I have numbered *seriatim* :—

(1)—It is by no means true that the English naturalists have based their statements upon Professor Schaafhausen's figures; for, as I have on two occasions publicly stated, Dr. Fuhlrott has been good enough to furnish us with both photographs and casts of the skull. (See "Lyell's Antiquity of Man," p. 82. "Man's Place in Nature," p. 141.)

(2)—I have given no opinion, nor to the best of my knowledge has any English anatomist, respecting the geological age of the Neanderthal skull, or any other, but have assumed the justice of Sir Charles Lyell's conclusions on that head. What I have affirmed, and still affirm, is, that the skull is the most ape-like human cranium I have ever seen, irrespective of any question as to its age.

(3)—Seeing that, according to Professor Mayer's own statement, both the coronal and lambdoidal sutures are present, it is not a matter of the smallest importance, in estimating the length of the sagittal suture, whether it is now discernible or not; since that suture could not be longer or shorter than the distance between the median portion of the coronal, and that of the lambdoidal suture, which, as I have already said, is only $4\frac{1}{2}$ inches. But, if the original skull really exhibits no remains of the sagittal suture, all I can say is that Dr. Fuhlrott's cast, which lies before me, is very deceptive; as it shows what are, to all appearance, very distinct traces of that suture; though

[1] "Unter allen bis jetzt als vorweltlich erkannten Schädeln am ähnlichsten sei." I am acquainted with no exact English equivalent for "Vorweltlich"—"Antediluvian" and "Preadamite" used to serve that purpose; but recent discussions render it inexpedient to make unguarded implications respecting either Adam or the Deluge.

it is not so plain as the coronal, and far less obvious than the lambdoidal suture.

(4)—I must ask, what has arching of the calvaria in the supra-occipital region to do with the "want of space" for the posterior lobes of the cerebrum? Surely a local bulging does not interfere with the flatness of the skull as a whole? And I have been careful to point out that "notwithstanding the flattened condition of the occiput, the posterior cerebral lobes must have projected considerably beyond the cerebellum."—"Man's Place, &c." p. 143.

(5)—As to the last paragraph (if it refers to any supposed opinion of mine) I can only account for it by supposing that Professor Mayer has not done me the honour to read what I have published on this subject. At least, it is inconceivable to me that he should have so written with the two paragraphs before him, which I will venture to quote:—

"In no sense then can the Neanderthal bones be regarded as the remains of a human being intermediate between men and apes."—(Man's Place in Nature," p. 157).

"In conclusion, I may say that the fossil remains of Man hitherto discovered do not seem to me to take us appreciably nearer to that lower pithecoid form, by the modification of which he has, probably become what he is."—(*ibid.* p. 159).

After the somewhat infelicitous introductory remarks, which I have just ventured to criticise, Professor Mayer proceeds to communicate the results of his own observations upon the skull. These I give at length, in order that the judicious reader may have the means, by comparison with what is already extant, of forming his own judgment upon the value of Professor Mayer's additions to our extant information:—

"The calvaria in question is dolichocephalic, the longitudinal measurement of it, from the supraciliary arch to the occipital spine amounting to 7″ 9‴. The contour of its circumference is of such a kind that a depression succeeds to the very considerable projection of the supraciliary arches, after which the frontal region slightly rises again, then sinks little, and next slightly ascending forms a flat parietal arch; this, descending backwards, sinks again, and then descends as a considerable convexity from the summit of the squama occipitis (the lambdoid suture of which is visible externally, and internally though but faintly), occupying almost the whole of the occipital squama.

"The beautiful arching of the occipital bone is remarkable from the circumstance that its crest and spine project but little, shewing a slight development of the muscles of the neck, and leading one to

ascribe, not the wildness of a supposed contemporary [vorgeblichen Zeitgenossen] of the Gorilla, but rather an oppressed slavishness, to the Düsseldorf Troglodyte."

But I have elsewhere (Man's Place in Nature, p. 142) quoted Dr. Fuhlrott to the effect that the superior semicircular line forms "a very strong ridge" in the Neanderthal skull; and I find this statement of the possessor of the cranium to be fully borne out by the cast. In these points, as in many others, the Neanderthal skull has a curiously Australian aspect: though I do not venture, on that ground, to infer any special affinity between the man to whom it belonged and the Australian race.

I should not feel myself on very safe ground if I endeavoured to follow Professor Mayer in his diagnosis of psychical peculiarities from the state of the spine and cristæ of the occipital bone. But surely, to deduce a man's "oppressed slavishness," from the condition of the muscular ridges on his occiput savours more of that spirit of drawing "weitgreifende Folgerungen," of which Professor Mayer accuses English naturalists, than anything that has been said on this side of the Channel.

But let us hear Professor Mayer further:

"In correspondence with this there is, of course, no question of a sagittal crest, or its projection; the place of the sagittal suture being, on the contrary, depressed. I might say: shew me a fossil human skull with a sagittal crest like that of the Orang-utan (the male—the female possesses it but slightly—see Mayer in Troschel's Archiv für Naturgeschichte, 1845), and I will grant you your descent from an ancestral *Pithecus*."

But is it really necessary to wear a sagittal crest in order to make out a title to a pithecoid pedigree? Does not Professor Mayer believe that the Chimpanzees have descended from an 'ancestral *Pithecus*'? Yet they lack the credentials upon which he insists—never a one yet having been able to show "a sagittal crest like that of an Orang-utan."

And Professor Mayer does not seem to be aware of a circumstance which makes his argument still more frivolous, viz., that certain male orangs are devoid of the sagittal crest.

Professor Mayer continues:

"Further, the linea semicircularis of the temples is also but slightly marked, which indicates but weak temporal muscles.

"The calvaria, indeed, possesses a solid consistence, and the hardness and smoothness peculiar to fossil bones, as well as a brownish colour, but exhibits no hyperossification; but two lamellæ with diploë

increasing posteriorly, so that on the lateral wall it is 2 lines thick, on the occiput 3 lines. The inner surface of the calvaria also indicates but moderate osseous development, the falx frontalis projecting but little; the falx sagittalis being entirely absent; the falx cerebelli ossea being but slightly developed, and the impressions of the central gyri, viz., two depressions on the inner lamella, corresponding to the superciliary arches and smaller impressions in the lateral wall, being still visible. The superior occipital fossa for the posterior lobe of the brain is, on the left side, deep but narrower, on the right side, broader, but flat. The groove for the arteria meningea media is still present below, but disappears above. The fossæ for the Pacchionian glands are tolerably large, especially on the right side, near the place of the sagittal suture. I may add that the fossa for the lachrymal gland on the malar process of the frontal bones of both sides is remarkably deep. Thus there is no particularly strong bony development of the skull; the disappearance of the sagittal suture externally as internally; that of the coronary suture almost wholly internally; the weakness of the lambdoid suture, further demonstrate this deficiency of bony growth. Thus far then, the characters of the fragment of the skull under discussion are not at all ape-like. Is this, however, not true of the large and broad projections of the supraciliary arches, to which so much weight is attached by Professors Schaafhausen and Huxley?

"In the superciliary arches a distinction must be carefully drawn between the tuberositas or crista superciliaris and the arching of the frontal sinuses behind them. Each may exist independently of the other. The crista superciliaris is in the apes, in the Gorilla especially, strong, and gives the face its ferocious expression, whilst at the same time the frontal sinuses are entirely absent! In our Neanderthal skull, on the other hand, there is no crista superciliaris such as is frequently met with in human skulls with exostosis of the diploë, where the frontal sinuses are absent, and the two, strongly osseous, laminæ of the os frontis are closely applied together. Consequently the projection of the superciliary arches in this cranial fragment constitutes no approximation to the type of the Ape or Gorilla." —pp. 2–4.

I must confess myself greatly perplexed to discover the relevancy of some of the arguments which Professor Mayer brings forward.

In which of the higher apes—Gorilla, Chimpanzee, or Orang—has he found an osseous 'falx sagittalis,' or 'falx cerebelli'? And if they are not found in the apes, what has their absence in the Neanderthal skull to do with the question?

Again, in the higher apes, the sutures, with age, disappear very completely; how then is their asserted absence in the Neanderthal skull evidence against its ape-like character?

Still more difficult do I find it to understand how the closure and disappearance of the sutures is to be regarded as arising from a want of bony matter. If the argument were worth anything, I should have thought it told the other way, seeing that more bony matter must be required to close a suture than to leave it open.

Thus the former part of the passage just quoted appears to me to be irrelevant; the latter part, on the contrary, is relevant enough, but, unfortunately, it is incorrect.

To the sentence—"The crista superciliaris is in the apes, in the Gorilla, especially, strong and gives the face its ferocious expression, whilst, at the same time, the frontal sinuses are entirely absent."—Professor Mayer has affixed a note of admiration in the original. And he has done well, for it expresses with great accuracy the feelings of the reader who happens to be aware that both in the Gorilla and the Chimpanzee the frontal sinuses may exist, and sometimes attain far greater absolute and relative dimensions than in man. There are to be seen, at the present moment, in the Museum of the Royal College of Surgeons, two bisected skulls, one of a Gorilla and one of a Chimpanzee, in which the frontal sinuses are enormous, their walls being no thicker, in proportion, than in man.

So much for Professor Mayer's facts and reasonings concerning the Neanderthal skull; I come next in order to his remarks on the accompanying bones appertaining to the rest of the skeleton.

"The (left) innominata is represented only by a part of the os ilium, which is injured superiorly. The anterior superior spine and the crest are strong; the iliac fossa is deep; the linea innominata projecting: the os pubis is for the most part wanting, the acetabulum is spacious, the greater ischiatic notch large but narrow, the lesser notch and the ischiatic spine are wanting; the tuberosity of the ischium is singularly turned upwards, forwards, and inwards, and moderately strong. The two thigh bones are similarly formed, about 17 inches in length, and therefore moderately long; strong, thick and heavy. They are both convex forwards, and somewhat twisted inwards below. This flexure is not normal, and is observable, like the inward flexure of the tuberosities of the ischial bones, in those who have been riders from their youth up.

"The angle of the femur [Winkel des femur] is 110°, its condyle and the trochanters are strong, the crista glutæorum is sharp, the internal condyle projecting, and both tubera of the condyles strong. The right

humerus is 11 in. 9 lines long, somewhat curved in its upper half; it is solid and heavy, but normal, the greater and lesser tuberosities and the linea aspera project strongly, also the condyles and the trochlea downwards: the fossa ant. major and minor, as well as especially the fossa posterior at the lower articular end are deep. Of the right ulna merely the upper part remains. It is convex backwards. Humerus and coronoid process are normal, as are the sigmoid and semilunar fossæ. If the radius (*sic*) were entire,[1] it would measure 10½ inches. The bones of the left arm are in a remarkable condition. Of the left humerus unfortunately only the middle and lower thirds exist. It is thinner than the corresponding part of the right humerus, the linea aspera is strong; while, on the other hand, the internal and external condyles are weaker. The trochlea is tuberculated (knorrig), and enlarged forwards, posteriorly sharp edged, the processus capitatus small, but also rough and tuberculated.

"The fovea anterior humeri major is broad and large. The fovea minor is almost flat. The fovea posterior especially deep and broad. The left radius is wanting, but it can only have been 8 inches 4 lines long. The entire ulna, in fact, is only 9 inches long, or shortened by 1½ inches, seeing that if normal it would have been 10½ inches long. The olecranon is very large, thick and tuberculated, its four articular impressions are unequal, and the coronoid process projects strongly. The fovea semilunaris for the head of the radius is only indistinct. The whole ulna is twisted longitudinally, so that the forearm was fixed in a prone position, the radius standing forwards, the ulna outwards. The carpal extremity of the ulna shewed nothing irregular."

Professor Mayer's conclusion from these malformations (of which it must be remembered Professor Schaafhausen had already given a sufficient account), is, that the Neanderthal Man had been a rickety child[2]—which might account for the peculiarities of the limbs, but not, so far as I can see, for those of the skull. However, Professor Mayer would get over this difficulty with ease, for he says (l. c. p. 5):—

"The prominence of the superciliary arches is in part, like the projection of the crista, occasioned by the corrugator superciliorum muscle, but this need but be weak if it has only to lift the already raised outer lamella of the frontal bone."

A severe critic might, perhaps, find something over-mechanical in

[1] The context seems to show that by 'radius' Professor Mayer here means "ulna." Prof. Schaafhausen speaks of the right radius as "perfect," but does not give its length.

[2] Prof. Schaafhausen, on the contrary, is careful to remark that the ulna "shows no trace of rhachitic disease"! Müller's Archiv. 1858, p. 458.

Professor Mayer's physiology: but, granting the premises, the conclusion is obvious. Given a rickety child with a bad habit of frowning (say from the internal flatulent disturbances to which such children are especially liable), and the result will be a Neanderthal man! Truly a "weitgreifende Folgerung!"

The man being accounted for, the next difficulty is to get him into the cave, and bury him in the loam covering its floor.

Professor Mayer admits that the bones were covered by at least two feet of loam, and were in undisturbed relation to one another (l. c. p. 19, 20.). He is quite clear that they were not drifted by floods into the cave (p. 20), or buried there in ancient, say preceltic, times, because the bones of other corpses, and the general attributes of old graves are absent (p. 21); and he concludes that the Neanderthal man must have crawled into the hole to die. The obvious inquiry follows, how did this singular person contrive to get buried under, at least, two feet of loam, after he had died there? And as the cave had an opening of only two feet in height, sixty feet up a vertical cliff, with only a very narrow plateau in front of it, it will be observed that the problem is not devoid of difficulties. Professor Mayer admits them, but meets them thus:—

"Streams of water, therefore, could only have reached the grotto from the precipitous heights which rise above it to the south, and since the opening of the cave lies to the north, they could only have got into it, carrying the loam with them, by rebounding." [durch Widerschlag] (l. c. p. 20.)

And now, having fairly got the man into the cave and covered him up by the 'rebounding' of cataracts of muddy water, who was he?

A 'Mongolian Cossack' of Tchernitcheff's corps d'armée is Professor Mayer's suggestion;—based upon three reasons: the first (p. 20) that the thigh bones are curved like those of people who spend their lives on horseback; the second (p. 21), that any guess is better than the admission that the skeleton may possibly be thousands of years old; the third, (p. 21-2) that, after all, the skull is more like that of a Mongol than that of an ape, or a Gorilla, or a New Zealander.

Thus the hypothesis which is held up to us by Professor Mayer as an example of scientific sobriety comes to this: that the Neanderthal man was nothing but a rickety, bow-legged, frowning, Cossack, who, having carefully divested himself of his arms, accoutrements, and clothes (no traces of which were found), crept into a cave to die, and has been covered up with loam two feet thick by the 'rebound' of the muddy cataracts which (hypothetically,) have rushed over the mouth of his cave.

Professor Mayer must, indeed, have a firm belief that anything is better than admitting the antiquity of the Neanderthal skull!

3. Professor Mayer has no reason to complain if I defend the views he has attacked with the weapons he has thought fit to select. It is much pleasanter, however, to argue scientific questions in another way; and although Professor Schaafhausen has impugned the accuracy of some of my own statements and conclusions in a much more formidable manner than Professor Mayer, I should err greatly if I treated with other than respect, the views of the careful and thoughtful observer to whom we are indebted for first bringing the now famous skull under the notice of anatomists.

Professor Schaafhausen has communicated to the "Societé d'Anthropologie" an abstract of a memoir which he had recently read before the Natural History Society of the Rhine and Westphalia on the Neanderthal skull.[1] In this the following passage occurs:—

"The assertion of Mr. Huxley that the posterior part of the cranium is still more anomalous than the anterior, is without foundation. According to this author, the upward and forward direction of the squama occipitis, the shortening of the sagittal suture, the straight edge of the temporo-parietal suture, and, in general, the flattened form of the cranium, which hardly permits one to understand the possibility of lodging the posterior lobes of a human brain therein, would approximate this cranium to that of an ape, still more than the conformation of the anterior frontal region. But Mr. Huxley has forgotten that all these peculiarities are equally met with in the crania of the lower races: the only character which belongs exclusively to the Neanderthal skull is the altogether animal ridge which bounds the orbital cavity above."

Seeing that my main object, in all that I have written upon this subject has been to prove that the Neanderthal skull differs only in degree from certain existing human skulls, I hardly expected the reproach conveyed in the last paragraph, which however errs, as I venture to think, in affirming that the peculiarities of the Neanderthal cranium are to be met with 'equally' in any human skull which has yet been described. It is quite true, as I have taken much pains to insist, that the features of the Neanderthal skull are simple exaggerations of characters to be met with in other human skulls: but though some human skulls are greatly depressed, none has yet been seen so depressed as it: though some have large superciliary ridges, none has them so large as they are in it: and though, finally, some have the occi-

[1] Sur le Crâne de Neanderthal, par M. Schaaffhausen. Bulletin de la Societé d'Anthropologie. Tome iv. p. 364.

put greatly inclined, none (except perhaps one of the Borreby skulls) has been shown to exhibit that peculiarity in so marked a degree as it does.

Professor Schaafhausen continues :—

" Lastly, Mr. Huxley's remark, that the two lateral sinuses, that is to say, the inferior limits of the posterior cerebral lobes are perfectly visible, is quite as erroneous : this observation is based on photographs : but in the specimen there exists only the commencement of the right sinus, where it takes its origin from the superior longitudinal sinus."

I greatly regret to differ from so competent an anatomist, who has further had the advantage from which I have been debarred, of examining the original specimen : but, after a re-examination of the photographs, and a careful study of the cast of the interior of the skull, which Dr. Fühlrott has been good enough to send me, I must stand by my original view, that the inferior limits of the posterior lobes of the brain are accurately deducible from the markings in the interior of the skull.

Professor Schaafhausen states that there exists "only the commencement of the right sinus where it takes its origin from the superior longitudinal sinus." On the contrary, both cast and photograph plainly show, not merely the *commencement* of the right lateral sinus, but fully an inch and a half of it, passing not only downwards but outwards. The outer end of this segment of the lateral sinus certainly indicates the line of attachment of the tentorium ; which again denotes the boundary of the right posterior lobe : and as both lobes are approximatively of equal extent, I do not think that my statement is other than well founded, supposing only the right sinus to exist.

However, it still appears to me that I can discern clear indications of the left, as well as of the right, sinus upon the materials at my disposal ; and, in any case, the posterior aspect of the cast of the interior conclusively shows the lower boundaries of both the right and the left posterior lobes.

Professor Schaafhausen further observes :—

" It is not less singular that Mr. Huxley should have found an Australian cranium comparable to that of the Neanderthal. For, according to the opinion of all naturalists (Becker, Martin, Lucæ, Ecker), the cranium of the Australian is narrow, elevated, and declining like a roof rapidly from the summit to the temples, whilst that of the Neanderthal is very much flattened, wide behind, and without any trace of the conformation indicated."

To this I can only reply that, however singular and opposed to ordinary opinion it may be, the Australian skulls to which I have

referred really do exist, and are open to the inspection of any person who chooses to examine them in the Museum of the Royal College of Surgeons.

Professor Schaafhausen concludes thus:—

"I remark besides that No. LXIII of Blumenbach's Decades Craniorum, which represents the skull of a Dutchman of the island of Marken (*Batavus genuinus*), presents a great resemblance to that of the Neanderthal."

I do not think that Professor Schaafhausen would have made this remark had he been disposed to consider with more favour what I have said respecting the marked peculiarity of the occipital region of the

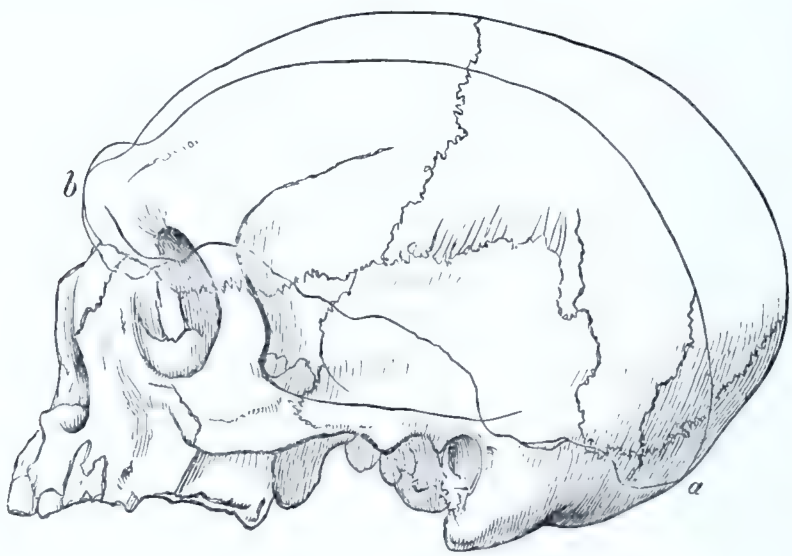

FIG. I.

Reduced copy of Blumenbach's figure o. a "Batavus genuinus." The contour of the Neanderthal skull, reduced to the same length, is drawn upon the figure; the glabellæ being made to correspond, and the superior curved line of the Neanderthal skull being adjusted to the point *a* of the other. The skulls are not reduced to the same scale, and hence this figure only gives the different proportions of the two.

Neanderthal skull. There is, it is true, a certain approximation between the skull in question and that from the Neanderthal in the rapid backward slope of the frontal region; but it is not closer than I have seen in many other skulls, and more particularly in one of an English sailor, long ago pointed out to me by Mr. Busk. On the other hand, the occipital region of the Batavian cranium, a faithful reduced copy of which is here given, (*fig.* I,) differs most remarkably from that of the Neanderthal man.

The superior curved line of the occiput is not represented in

Blumenbach's figure, but it cannot well be higher than the point (*a*). If now, the glabello-occipital lines of the Neanderthal skull and it be made to coincide, as in *fig.* 1, the prodigious difference between the two will become obvious ; the occiput of the Dutch skull projecting backwards far beyond the point (*a*), while, on the other hand, that of the Neanderthal skull slopes upwards and forwards from it.

What appears to me to have misled Professor Schaafhausen is the circumstance that if the contour of the Neanderthal skull be simply superimposed upon that of the "Batavus genuinus" the two will nearly coincide. But the fallacy of concluding from this circumstance, that the skulls have a real similarity is at once demonstrated by the fact that, when the contours are thus superimposed, the superior curved line of the occiput of the Neanderthal skull is nearly on a level with the summit of the lambdoidal suture of the other. In other words, the more the two skulls are made to agree in front and above, the less their correspondence behind and below.

M. Pruner-Bey, in some observations appended to Professor Schaafhausen's communication, expresses the opinion that the Neanderthal skull is "undoubtedly that of a Celt."

"In the first place it belonged to a person of high stature ; it is voluminous and dolichocephalic ; it presents the groove at the posterior third of the sagittal suture common to the Celts and the Scandinavians ; lastly, the occipital projection is equally characteristic of the two races."

But the bones found with the skull lend no countenance to the opinion that the Neanderthal man was above the middle stature of five feet six inches ; and as the other two characters are avowedly common to Celts and Scandinavians, I can hardly think them good diagnostics of Celts. Australian crania may be found with the occiput quite similarly formed to that of the Neanderthal ; and, as to the capacity of the skull, I shall demonstrate, by and bye, by the help of casts, that some Australian skulls were certainly as large.

M. Pruner-Bey seems to incline to the hypothesis that the Neanderthal man was an idiot : but I confess I find much weight in the pithy reply of M. Broca :—

"Idiocy, competent to produce a cranium of this kind, is necessarily microcephalic ; now this skull is not microcephalous, therefore it is not that of an idiot."

4. Mr. Turner's careful essay appears to me to be one of the most valuable contributions we have had upon this subject. By comparison with a skull from St. Acheul, Mr. Turner shows the existence of the closest resemblance between the Engis cranium, and one from the valley of the Somme, which there is no reason to think older than the

Roman period, and his statements fully bear out the conclusion at which Mr. Busk and I arrived, that the Engis specimen is a fair average human skull.

With regard to the Neanderthal skull Mr. Turner remarks—

"The Neanderthal skull unquestionably possesses a very remarkable shape, one which sufficiently distinguishes it from other known crania. But we must inquire whether its anatomical characters are altogether exceptional. Is it not possible, by carefully examining an extensive collection of skulls, such as are presented to the anatomist in a large museum or dissecting room, to find crania closely allied to it in some of those features which are regarded as most distinctive?"

This is the precise question which I asked myself when I first undertook to investigate the matter, and I am rejoiced to find that a careful observer, like Mr. Turner, arrives, by independent observation, at results similar to my own. Thus Mr. Turner finds, and partly figures, four modern British crania with very projecting superciliary ridges; though, as he is careful to observe, "none of them exhibit so massive a form at the external orbital processes as the Neanderthal skull."

He shows also, that some modern British crania have the forehead very retreating, and that many combine this character with a sloping occiput, so as, in these respects, much to resemble the Neanderthal skull.

Mr. Turner makes the important and just remark:—

"It would be quite possible to arrange from materials to which I have access, a series of modern British skulls, in which the variation may be traced from a well-marked posterior occipital bulging to a configuration of the upper occipital region closely approaching the form of the Neanderthal skull. In the skull cap represented in fig. 3, the diminished occipital convexity is almost equal to that of the last-named cranium."

And concludes with the following words:—

"From the comparison which has thus been instituted, I have no hesitation in saying that, although we may not be able to produce another skull possessing a combination of all those characters which are regarded as so distinctive of the Neanderthal skull, yet the examination of an extensive series of crania will shew us that these characters are closely paralleled, not only in the crania of many savage races now existing, but even in those of modern European nations.

"How cautious therefore ought we to be in generalising either as to the pithecoid affinities or psychical endowments of the man to whom it appertained. It is as yet but an isolated specimen; of its history,

prior to the day of discovery, we are altogether ignorant, its geological age is quite uncertain. In coming to any conclusion, therefore, we have no facts to guide us save those which are furnished by an examination of its structural characters and whatever marks of degradation these may exhibit, yet they are closely paralleled on the crania of some of the men, and women too, now living and moving in our midst."

With all this I cordially concur, desiring only to add a caution as to confounding the evidence of the existence of pithecoid characters, with the conclusions that may be based on that evidence. If the dissector of Jeremy Bentham had found a *levator claviculæ*, or a couple of bellies of the *flexor brevis digitorum* arising from the tendons of the deep flexors of the foot, as is sometimes the case in man, he would have had a perfect right to say that these were pithecoid characters; but

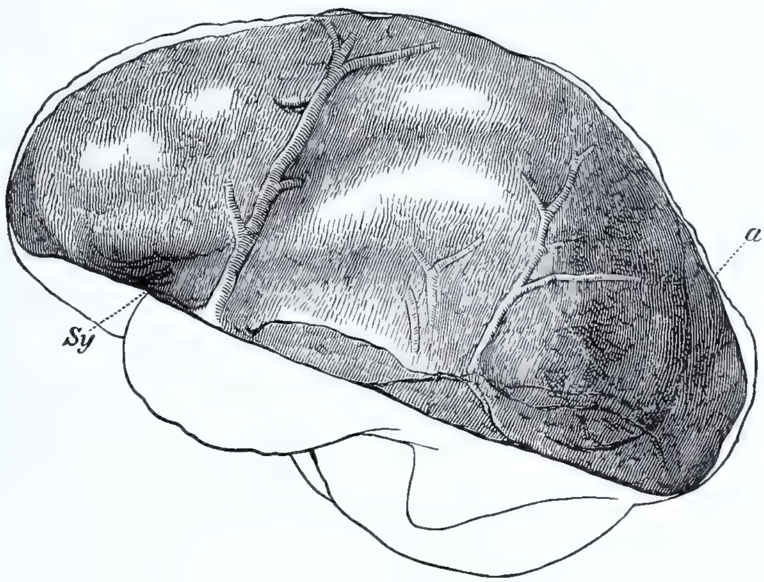

FIG. 2.

Side view of the cast of the interior of the Neanderthal skull reduced to one half of the natural size. The outline represents the contour of a like cast of an Australian skull in the Museum of the Royal College of Surgeons (No. 5331) reduced to the same scale. *a*. Cast of the inner face of the lambdoidal suture. *Sy*. the Sylvian fissure.

it by no means follows that he should have supposed the philosopher to be the 'missing link,' or a *homo pithecoides* (Mayer). And, in like manner, the prominent superciliary ridges, the retreating occiput, and so forth, of the Neanderthal skull, are, to my mind, most indubitably pithecoid characters; though I need hardly repeat the opinion, which I have so strongly expressed elsewhere, that the Neanderthal man was in no sense intermediate between men and apes.

The duty of the anatomist appears to me to lie as little in eagerly

building theories upon these variations of human structure, as in ignoring them when they are obvious. Let them be noted and estimated at their just weight—the future will tell us their meaning.

To sum up the result of a careful study of the extant materials so far as they are accessible to me, and of all that has been written on the subject, I think it may be said :—

That the Neanderthal skull exhibits the lowest type of human cranium at present known, so far as it presents certain pithecoid characters in a more exaggerated form than any other ; but that, inasmuch

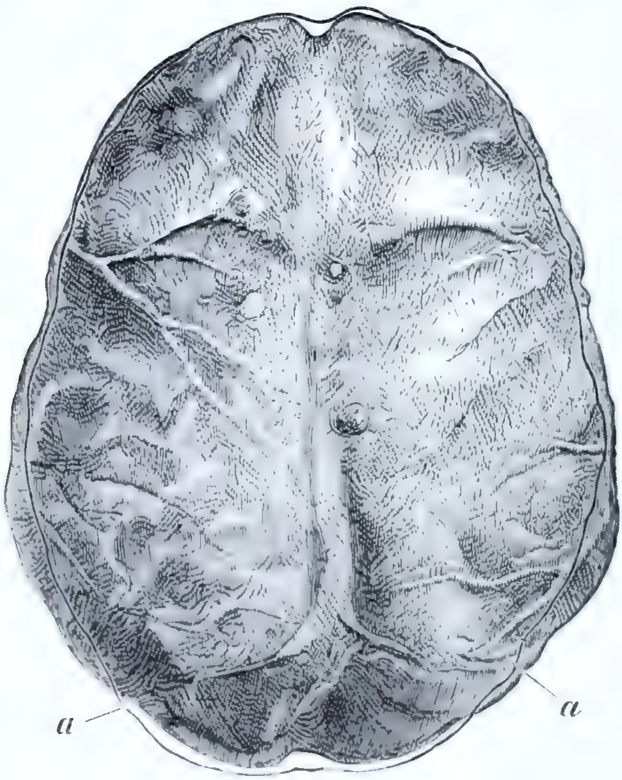

FIG. 3.

Represents the same objects as Fig. 2, viewed from above ; scale the same. *a a.* as before.

as a complete series of gradations can be found, among recent human skulls, between it and the best developed forms, there is no ground for separating its possessor specifically, still less generically, from *Homo sapiens.* At present, we have no sufficient warranty for declaring it to be either the type of a distinct race, or a member of any existing one ; nor do the anatomical characters of the skull justify any conclusion as to the age to which it belongs.

It seems difficult to believe that there now remains very much more to be said about the Neanderthal man's skull ; but we owe to Professor Schaafhausen some interesting information respecting his brain.

Professor Schaafhausen, it appears, obtained Dr. Fuhlrott's permission to take a cast of the interior of the Neanderthal skull. Of the reproduction of the form of the cerebrum thus obtained, he says:

"There is a great resemblance to that of an Australian presented to the Society at the same time, so far as the slight development of the brain is concerned. The latter cast even presents somewhat better dimensions. The following is the result of the comparative measurement of the casts.

	Length of hemispheres.	Width of anterior lobe.	The greatest width.	The greatest height.[1]
Neanderthal . .	173mm	112m	136m	66m
Australian . . .	164	100	125	77

M. Lucæ has made out that the weight of the European brain exceeds that of the Australian on the average by 300 grammes. As to dimensions, it is neither in length, nor in height, that the former considerably exceeds the latter, but in width. Thus this difference of the races is already manifest in the highest antiquity, when our countries were inhabited by men who, in intelligence, were on a level with the Australian savages of the present day."

I am indebted to Dr. Fuhlrott for what I presume to be a copy of the cast thus obtained by Professor Schaafhausen, and the accompanying woodcuts (Figs. 2 and 3) give two views of it, reduced to one half the natural size. With each view is represented the contour, under the same aspect, of the cast of the interior of one of those depressed Australian skulls in the Museum of the Royal College of Surgeons, to which I have already referred. The resemblance between the two is at once seen to be very striking. The Australian rather exceeds the Neanderthal brain in length (7·1 inches to 6·85 inches), but, on the other hand, it is narrower at its widest part (5·3 inches to 5·45 inches), and the length of a vertical arch taken over the highest parts of the two casts from corresponding points on their lateral surfaces is slightly less in the Australian (9·3 inches to 9·6 inches). Again, the transverse contour, such as would be seen by viewing the casts from behind, is more pentagonal in the Australian, more evenly curved in the Neanderthal brain; and both the anterior and the posterior lobes are more flattened above and less rounded at their ends, in the Neanderthal cast. But all these differences sink into insignificance if compared with those which separate the Australian brain-cast in question, from others in the same collection.[2]

[1] Taken at the line which joins the anterior and the posterior lobes.

[2] If, from the close resemblance of so much as can be reproduced of the cast of the Neanderthal skull to the corresponding part of the Australian, we may be permitted to

Thus, it appears to me, that the conclusion expressed in Prof. Schaafhausen's concluding paragraph is not borne out by facts, for the brain of the Neanderthal man is certainly not nearly so different from some Australian brains, as the extreme forms of Australian brains are from one another.

The "Crania Helvetica" of Professors Rütimeyer and His has come into my hands since the above was in type. Among the large series of ancient and modern crania figured in this elaborate and valuable work, I have only been able to find one which at all approaches the Neanderthal skull. It is that represented in the plate B. III, and is derived from Berolles, Canton Vaud. Ascribed to the Burgundian period, it is regarded by Rütimeyer and His, as a "mixed form" between their Sion and Hohberg types, or, in other words, as Celto-Roman. This skull, however, does not come nearly so close to the Neanderthal cranium as some of the Borreby and some of the Australian skulls do.

conclude that the like similarity obtained in the missing portion of the former, the Neanderthal cranium must have had a much larger capacity than the minimum (75 c. i.) I ventured to assign to it; for the cast of the Australian skull displaces $87\frac{3}{4}$ cubic inches of water. The maximum capacity of Australian skulls given by Morton is only 83 cubic inches, while the minimum sinks to 63 cubic inches.

XXXVII

ON THE ANGWÁNTIBO (ARCTOCEBUS CALABARENSIS, GRAY) OF OLD CALABAR.

Proceedings of the Zoological Society oj London, 1864, *pp.* 314–335.

(PLATE XXVIII. [PLATE 39].)

ON the 25th of April, 1860, Dr. John Alexander Smith read before the Royal Physical Society of Edinburgh a "Notice of the 'Angwántibo' of Old Calabar, Africa—an animal belonging to the family *Lemurina*, and apparently to the genus *Pérodicticus* of Bennett."

The specimen from which this notice was drawn up was sent home by the Rev. Alexander Robb, who, in a letter dated July 28th, 1860, which is quoted by Dr. Smith, says, "Another specimen which I procured I handed to Mr. Thomson, who, I believe, sent it to Mr. Murray."

This specimen my friend Mr. Murray was kind enough to transmit to me for examination, some two years ago; but I have unfortunately been prevented by the pressure of other occupations from undertaking the investigation until now.

The most important passages in Dr. Smith's description of his specimen, which, like mine, is of the male sex, are the following:—

"The Angwántibo is covered with a thick and long wool-like hair, which becomes short and thin on the face and on the extremities, the inner sides of the fore and hind hands being free from hair. The hair is of a dark grey colour at the base, and the upper third, or so, of its length is of a light brown or fawn-colour, the terminal points being of a darker brown; this is the general character of the fur of the upper parts of the body and limbs. The face in front of the eyes is rather darker in colour; but the sides of the head are lighter, and the chin and throat are nearly white. The inner surface of the

limbs is also lighter, as well as the whole under surface of the body; the grey hairs having their distal half of a light fawn colour, and in some places nearly white. The specimen having been for a long time preserved in spirits makes it a little difficult to get at the minute details of colour. There are no stripes or markings on the back, or other parts of the body, to be observed on this animal, as on the *Stenops tardigradus* of the East Indies—its general appearance being more uniform over the surface, although somewhat mottled in character, from the hair varying in colour at base and apex.

"The body of the Angwántibo is slender, and measures $10\frac{1}{2}$ inches in length from the point of the muzzle to the extremity of the very short tail, which is completely hid in the long fur of the body, and measures only about $\frac{1}{4}$th of an inch in length. This animal is a male, the penis, which is supported apparently by a small bone, projecting upwards and forwards from the rounded scrotum.

"The head is oval and rounded, tapering rapidly in front of the eyes: the muzzle protruded, full or blunt, and rather prominent. The breadth of the head in front of the ears is about $1\frac{1}{2}$ inch; in front of the eyes about $\frac{3}{4}$ths of an inch. The length from the mesian line of the nose to the anterior part of the meatus of the ear is $1\frac{3}{4}$ inch; from point of nose to anterior angle of eye is $\frac{3}{4}$ths of an inch; from anterior angle of eye to point of opening of ear $1\frac{1}{8}$ inch, the total length of head from muzzle to back part being nearly $2\frac{1}{2}$ inches.

"The eyes are rather full and large, the opening of the lids measuring $\frac{1}{2}$ an inch in length; the distance between the eyes at their anterior angles is $\frac{1}{2}$ an inch. They are rather prominent forwards, and very slightly lateral.

"The ears are erect and patulose, rather large and rounded in outline, without emarginations, measuring about $\frac{3}{4}$ths of an inch across from before backwards, and also from above downwards; they seem to be naked internally, and slightly covered with short hair externally. In this specimen they are nearly naked, especially on the inner surface. There are two transverse abrupt parallel projecting ridges of cartilage, each measuring $\frac{1}{12}$ths of an inch in length, in the free cartilage above the external opening of the meatus.

"The external openings of the nostrils are rather lateral, and are sinuous, curved upwards and inwards towards the median line of the full and rounded snout; and there is a groove between them running down to the front of the upper lip.

"The tongue is long and rounded in front, and rather rough, being covered with small papillæ. Immediately below the tongue is the projecting lamina, covered with a horny cuticle and resembling

a smaller bird-like tongue, which springs from the frænum, and projects forwards about $\frac{3}{8}$ths of an inch in length, reaching to within $\frac{1}{4}$th of an inch of the point of the tongue itself. This horny lamina measures about $\frac{1}{4}$th of an inch in breadth across its root or base, and about $\frac{1}{8}$th of an inch across its free or front extremity, which is divided into nine sharp terminal points or filaments . . . . Below the tongue and this supplementary organ the mucous membrane lining the floor of the mouth has a slightly free margin, projecting along the sides of the gums of the lower jaw, in which, apparently, the ducts of the submaxillary glands (Wharton's ducts) open into the mouth.

"The neck is rather short and slender. There is no appearance on the back of the neck of this specimen of the spinous processes of the five last cervical and first dorsal vertebræ piercing through the horny integument of the back, with a weak horny covering, as described by Van der Hoeven of the *Stenops potto*.

"The limbs are very slender and nearly equal in length, the hinder extremities being a little larger and stronger in their development than the anterior. The fore hands are thinly covered with short hair on the dorsal, and are bare of hair, or naked, on the palmar surface. The thumb is much larger than any of the other fingers, to which it is opposed. There is a large rounded fleshy and horny tubercle, nearly $\frac{1}{4}$th of an inch broad at its base, which projects about $\frac{1}{8}$th of an inch from the base of the thumb on the inner side (near the centre of the hand). Immediately opposed to it, and of equal size, or a very little larger, is another apparently simple tubercle, rising from the outer side (next the thumb) of the base of the clustered fingers; this, however, is the rudimentary index finger, its free extremity projecting only about $\frac{1}{8}$th of an inch. It is supported by a short metacarpal bone, with a full and rounded extremity, to which are attached *two* small, or rudimentary, phalanges; each of the other fingers (not including the thumb), having *three*. This rudimentary index finger has no nail; there is simply a minute marking like a cicatrix, or rather a mere short depressed smooth line, an indication of where a nail should be. The nails of the thumb and of the fingers are all thin, flat, and rounded or ovate, like those of the human hand, and are not extended beyond the points of the fingers. The remaining three fingers are slender and prolonged, and the first phalanges are all conjoined by the integuments, the two distal phalanges of each finger, alone, being free. The index or second finger (considering the thumb as a finger) is, as already described, merely like a tubercle rising at the base of the others. The third finger is the smallest of

the three other fingers, and also the shortest; the fourth (or middle of the developed fingers) is the longest; and the fifth, or last, is longer than the third. The hands are each divided into two opposing portions—the thumb with the tubercle at its base being opposed to the other fingers with the tubercle-like index at their base, the thumb itself being opposed to the fourth, the middle or longest of the fingers.

"The posterior hands, or feet, are rather larger and stronger than the anterior ones, and are each divided into two opposing portions—the one consisting of the thumb, with a large rounded fleshy tubercle projecting from the inner side of its base (as in the fore hand), and the other portion, formed of the remaining four fingers, the first phalanges of which are also conjoined, being covered by the integuments as in the hand. There is a comparatively smaller fleshy tubercle, somewhat like the undeveloped index finger of the fore hand, projecting from the outer side of their base, which is opposed to the tubercle at the base of the thumb. The nails of the thumb and fingers are thin, flat, and rounded or oval in form, like those of the fore hand, with the exception of that of the second finger, (counting the thumb as the first), which is narrow, convex, sharp-pointed, and claw-like, and extends nearly to the point of the third finger . . . The whole length of the free extremity of the finger is half an inch, including the claw-like nail, which measures rather less than a quarter of an inch."

I have quoted Dr. Smith's clear description at length, because it applies, in almost every particular, to my own specimen, though there are some points of difference which I shall now proceed to note.

I find a pale band running down the median line of the face from the brow to the end of the nose, where it divides and sends a short lateral branch along the alæ of the latter; otherwise the characters of the pelage are quite those given by Dr. Smith.

I may remark in addition, however, that there are no vibrissæ nor defined eyebrows. A patch of short dark brown hairs, with interspersed, almost black longer ones, grows upon the inner half of the upper eyelid; and two tufts of hair, 0·3 in. long, project horizontally, one from the point of the tragus, the other from the region of the antitragus, or lower part of the pinna of the ear. The inner surface of the ear is, for the most part, covered with fine short hairs.

The pinna of the ear (fig. 1) is not flattened and directed outwards, but is curved, so that its posterior surface becomes convex, while its outer margin is bent forwards, so as to be placed midway between the

[PLATE 39.]

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J. Wolf. del. A. Hammond, lith

ARCTOCEBUS CALABARENSIS.

front and the hinder boundary of the external ear. Hence the aperture of the external ear is directed forwards as much as outwards. The pinna has no distinct lobule; the tragus (*t*) is very small; the helix (*h*) is represented only by the thin edge of the pinna; the antihelix (*a.h*) is more distinct, and divided in front and above into two branches; at its base, inferiorly, a small antitragus appears. The fossa innominata, which separates the helix and antihelix, is obsolete, except inferiorly, where it forms a deepish pit behind the antihelix.

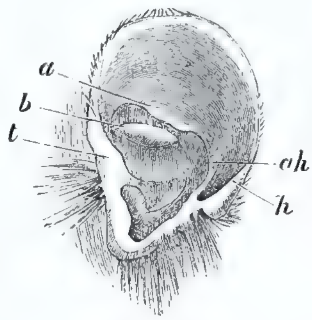

FIG. 1.
The left ear of the Angwántibo.

The two singular transverse ridges (*a*, *b*), which lie above the auditory meatus and anterior to the upper end of the antihelix, described and figured by Dr. Smith, are 0·25 inch long and about 0·1 inch high; they are separated at their bases by an interval of about 0·1 inch, but their free edges approach more closely. Fine hairs spring perpendicularly from the opposed margins of these ridges, and interlock with one another.

The length of the body is only 9·8 inches, instead of 10½ inches. The tail, however, has the same length (0·25); and the other measurements are very similar to those of Dr. Smith's specimen, thus :—

	inches.
The breadth of the head in front of the ear is	1·5
The breadth of the head in front of the eyes is	0·8
Mesian line of nose to anterior part of meatus auditorius	1·75
Point of nose to anterior angle of eye	0·75
Anterior angle of eye to ear	1·1
Total length of head	2·5
Eye-slit	0·4
Distance between inner canthi	0·45
Ear, antero-posteriorly (when flattened out)	0·75
Ear, vertically	0·8

The measurements of the limbs also agree very well with those given by Dr. Smith (*l. c.* pp. 184, 185). Thus I find the distance from the

	inches.
Point of shoulder to the elbow to be	2·15
Elbow to wrist	2·15
Wrist to point of fourth finger	1·25
Great trochanter to knee	2·45
Knee to ankle	2·45
Foot from ankle-joint to point of fourth toe	1·5

Dr. Smith gives :—Arm $2\frac{1}{4}$ inches; forearm $2\frac{1}{4}$; hand $1\frac{1}{4}$; thigh $2\frac{1}{2}$; leg $2\frac{1}{2}$; foot $1\frac{1}{2}$.

The differences obviously lie within the limits of individual variation.

Dr. Smith's description of the nostrils and of the snout fits the present specimen very well; but not so the figure given at page 188 of his paper, in which the snout is far too blunt, and the nostrils have too little curvature. Of the tongue I shall speak fully by and by; in general it agrees with Dr. Smith's description.

The spinous processes of the cervical vertebræ do not project in the manner described by Van der Hoeven in the Potto, though they can be readily felt through the skin. Dr. T. Strethill Wright's figures of the hand and foot of Dr. Smith's Angwántibo would very well represent those of the present specimen; nor need any modification be made in the description of those parts. I may remark, however, that short hairs are developed upon the dorsal surface of the distal phalanges, as of the rest.

The disposition of the hands and feet and of their digits, however, calls for some special notice.

All the digits were strongly flexed. The exertion of a considerable force was necessary to extend them; and when that force was removed, they at once returned to their flexed attitude. Left to itself, the hand assumes the prone position, with the thumb inwards, the fingers outwards; under like conditions, the dorsum of the foot is turned as much outwards as upwards, and the fibular edge of the metatarsal region downwards (fig. 2, B).

The distal part of the foot can be so rotated that the dorsal region of the metatarsus is turned completely upwards and completely outwards; but left to itself, it returns to the position just described.

The sole of the foot is formed behind, as usual, by the tuberosity of the calcaneum, and is bare; in front, where the hallucal and digital divisions of the foot diverge, there is a callous oval projection (fig. 2, C, *a*) supported by a large sesamoid bone. The skin is bare on this projection; but between it and the ball of the heel is a narrow hairy band.

Dr. Smith does not mention the circumstance; but, in the hand of the present specimen, the two distal free phalanges of the third digit are not parallel with those of the fourth and fifth digits, but are directed obliquely inwards (fig. 2, A).

With Dr. Smith, I find only two phalanges in the index finger (the second being very short and slender), and no trace of any nail, the

only marking on the exterior of the digit being that produced by the projection of the end of the metacarpal bone.

The proximal phalanx of the index finger is 0·15 inch long; the distal rather less than 0·1 inch.

Thus far the differences between my specimen and that described by Dr. Smith are of no moment; but on passing to the dentition I find, with a complete general correspondence, a solitary discrepancy which I cannot account for.

Dr. Smith says of the upper incisors:—"Two together (in pairs), with intermediate edentulous space; first incisor the smallest; the second nearly twice as large as the first."

In the specimen under description, on the other hand, the upper incisors are strictly equal in size; and the proportions of the two

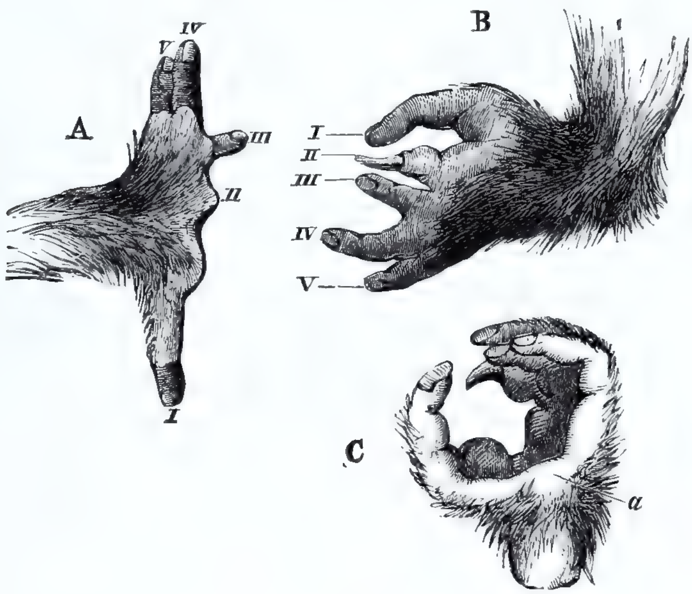

FIG. 2.

A. The left hand: The digits artificially extended as far as they will go.
B. The left foot in its natural position, seen from without.
C. The same, seen from below.

teeth noted by Dr. Smith are the more remarkable, as they do not obtain in any other Lemurs. When, as in *Nycticebus* and *Tarsius*, the upper incisors are unequal, it is the outer which is the smaller.

In the face of the resemblances of size, proportion, pelage, and sex between the two specimens of Angwántibo, it is difficult to admit that this singular difference can have more significance than an individual variation. However this may be, the characters of the teeth of the Angwántibo are so well shown in the present specimen

that I shall describe its dentition at some length, and compare it with that of the other Lemurs.

The series of teeth belonging to the adult dentition is complete (except the right outer incisor, which is broken off at the root), and the crowns are not at all worn. The total number of the teeth, as in the majority of the Lemurs, is 36; and the dental formula is—
$i. \frac{2-2}{2-2}$; $c. \frac{1-1}{1-1}$; $pm. \frac{3-3}{3-3}$; $m. \frac{3-3}{3-3}$.

In the upper jaw (A, C, fig. 3) the incisors (*i*) are set in a nearly straight transverse line, at the outer ends of which are the canines (*c*). The distance from the outer edge of one canine to that of the other is 0·4 in. The inner edges of the grinders (1–6) are also arranged in straight lines; the distance of the right and left series, anteriorly, is 0·3 inch, posteriorly, 0·4; while the length of the series is 0·7 inch. The five hinder grinders are close together; while the first premolar is separated from the second by a slight interval—less, however, than that which separates the first premolar from the canine.

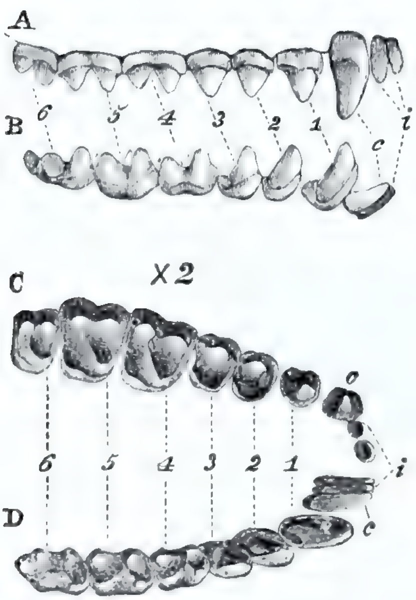

FIG. 3.
Right dental series of both jaws of *Arctocebus calabarensis*.
A and C, upper; B and D, lower jaw.

The median incisors are distant from one another about $\frac{1}{16}$th of an inch. The outer incisors are separated from them by less than half that space; but are as near the canines as they are to the median incisors. The incisors are not more than $\frac{1}{20}$th of an inch in breadth, and are chisel shaped, with their outer angles rounded off.

The inner and outer incisors are as nearly as possible equal in size, and their crowns are not more than $\frac{1}{10}$th of an inch long. The pointed and curved canines are between $\frac{1}{5}$th and $\frac{1}{6}$th of an inch long, and measure 0·1 inch antero-posteriorly. Their front edges are convex, the posterior concave, and both are sharp and cutting.

There is a rudimentary cingulum on the outer side of the base of the canine, both internally and externally, and the inner face of the tooth is produced into a vertical ridge. The base of each of the premolars measures about 0·1 inch antero-posteriorly; viewed from without (fig. 3, A) each looks like a shorter canine, with the cingu-

lum much more marked, and so greatly developed backwards as to give rise to a "talon" (heel, or posterior basal process). From within, or above (fig. 3, C), the cingulum appears still better developed, in accordance with the increased breadth of the base of the tooth. The base of the first premolar (1) is not much thicker than that of the canine (0·083); but in the second (2) it measures 0·1 inch, and in the third (3) 0·13 inch. In this last tooth, therefore, the crown is rather wider than it is long. Opposite the end of the ridge on the inner surface of the principal cusp, which is present in the premolars, as in the canine, rises, within the cingulum, a second, minute or rudimentary cusp; while the cingulum itself is produced internally and behind into a third similar cusp. Thus the second and third premolars are tricuspidate, two cusps being internal and one external; the ridge which runs down the inner face of the latter joins the antero-internal rudimentary cusp.

The two anterior molars (4, 5) are larger than the premolars, measuring 0·15 inch long by 0·18 wide. The hindermost (6), on the other hand, is hardly larger than the last premolar, being 0·1 inch long by 0·13 inch wide.

The two anterior molars are each surrounded by a cingulum, like the premolars, but are quadricuspidate. As in the premolars, the outer cusps are larger than the inner; but the disproportion is far less. The last molar has the postero-internal cusp rudimentary.

If the crowns of the molars and premolars be compared together, it will be found that the former differ from the latter, mainly, in the great relative development of the parts answering to the posterior basal process and the rudimentary cusps of the premolars.

Of the two outer cusps of the molars, the anterior represents the principal cusp of the premolars; the posterior is an additional growth from the outer side of the heel, which has now become as large as the anterior division of the tooth. The two inner cusps are readily identifiable with the rudimentary cusps of the premolars, the only important difference being that the antero-internal cusp is now separated by a groove from the cingulum, instead of rising directly from it. The oblique ridge connecting the antero-internal with the postero-external cusp appears to be a new development, not represented in the premolars. By its appearance, the molars of the Angwántibo acquire the pattern which is so obvious in Man and in the Anthropomorpha, but which is absent in all the Old-World Apes and in most of those of the New World.

In the lower jaw (B, D, fig. 3), the proclivous, close-set incisors and incanes occupy a space of 0·15 inch. The grinding series is 0·7

inch long; and the first premolar is separated from the second by an interval about equal to that which exists between it and the canine.

The incisors are laterally compressed, and, at their bases, longer from before backwards than they are from side to side. Their front faces are convex from above downwards; their posterior faces convex from side to side, but concave from above downwards, and so inclined to the front faces that the upper rounded edges are sharp. The canines are like the incisors, but somewhat broader, thicker, and sharper at the edges. The cingulum of the incisors and canines, unmistakeably present, and, in its ordinary place on the backs of the teeth, becomes confounded with their outer edges higher up, so that their front faces might be said to be almost wholly, if not quite, "*subcingular.*"

The first premolar has the crown 0·17 inch long, and therefore is a much larger tooth than the canine. It is recurved and pointed, and has a sharp anterior and posterior edge; the cingulum, traceable on both the inner and outer faces, rises much higher in front than behind, and is produced posteriorly into a slight cusp-like talon. The inner face of the tooth has an obscure rounded longitudinal ridge.

In the other two premolars, which are successively shorter than the first, the form of the tooth is fundamentally similar; but the base becomes broader, the inner ridge more definite and slightly angulated, and the posterior basal process of the tooth more distinct, and obscurely tuberculated, internally and externally.

Each of the three molars has about the same length (0·15 inch); the two anterior ones are 0·1 inch broad and quadricuspidate; the last, a little narrower, is quinquecuspidate; the fifth tubercle being median and posterior.

A well-marked transverse ridge connects the antero-external with the antero-internal, and the postero-external with the postero-internal cusp; and besides these an oblique curved ridge connects the postero-external with the antero-internal cusp. The cingulum is well developed, and there is an anterior basal process, whence a ridge rises to the antero-external cusp.

This ridge and the oblique ridge before-mentioned so connect the other ridges and cusps, that the grinding face of the tooth exhibits an almost doubly crescentic pattern—a circumstance of no small interest, if one reflects how extensively this doubly crescentic pattern obtains among other Mammalia. And, again, the foregoing analysis of the form of the molars shows that, different as the patterns of the

grinding surfaces of the upper and lower molars appear to be at first sight, they are really arranged upon much the same scheme.

Furthermore the transition from premolar to molar is effected in the same way in the lower as in the upper molars—by the development of cusps which are rudimentary in the premolars, and by the appearance of an oblique ridge.

The dentition of the genera *Loris* (*Stenops*), *Nycticebus*, *Perodicticus*, *Otogale*, *Galago*, and *Otolicnus*, resembles that of the Angwántibo in all essential particulars, but presents certain very interesting minor deviations.

In *Loris* the third premolar differs much from the first molar in both jaws; and the last molar of the upper jaw has its internal posterior cusp well developed, so that it is quadricuspid. The last molar of the lower jaw is quinquecuspid. The oblique ridges of both upper and lower molars are well developed; but, in the lower jaw, they do but just reach the anterior internal cusp.

In *Nycticebus javanicus* the oblique ridges are well marked in the upper molars, sometimes less distinct in the lower ones. Out of four skulls, the inner posterior cusp of the hinder upper molar was obsolete in three, and very small in the fourth. In the lower jaw, the fifth cusp of the last molar was very small or obsolete in three, while in the fourth (the same as that which had the inner posterior cusp of the last upper molar developed) it was distinct.

The dentition of *Perodicticus potto* (fig. 4), it is important to note, differs more from that of the Angwántibo than either of the preceding. For the posterior upper molar is short and wide, so as to have a transversely elliptical crown, which has only two cusps, the posterior external, as well as the posterior internal cusp having disappeared. In addition to this, the hinder upper molar is set further out than the other molars, and the hinder lower molar has only four cusps.

In all the species yet mentioned, as in the Angwántibo, the last premolar has but a short heel, and differs considerably from the first molar. But in *Otogale pallida*, *Galago sennaarensis* (fig. 5), *G. maholi*, *G. allenii*, *Otolicnus garnettii*, and *O. crassicaudatus* the heel of the hinder premolar above and below becomes so large and cuspidate as to assume the form of a quadricuspidate molar. This is particularly well seen in *Galago sennaarensis* (fig. 5) and *G. allenii.* In the latter species, even the second premolar acquires a great heel, so that the transition from canines to molars is quite insensibly graduated.

In *Galago minor*, on the other hand, the third premolar is as different from the first molar as in the Angwántibo.

With regard to the other teeth, the hindermost upper molar of *Otogale pallida* is quadricuspidate, though the inner posterior cusp is low, as in the first and second molars.

In the lower jaw the fifth cusp of the last molar is distinct, and the oblique ridges do not reach the antero-internal cusp.

In *Galago sennaarensis* the inner posterior cusp of the last upper molar is obsolete; but the fifth cusp of the last lower molar is well developed and ridge-like. In this species the lower molars might be

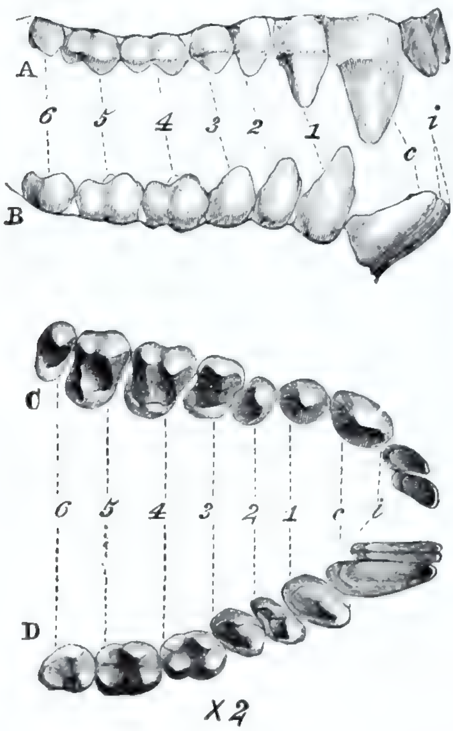

FIG. 4.
Right dental series of both jaws of *Perodicticus potto*.
A and C, upper; B and D, lower jaw.

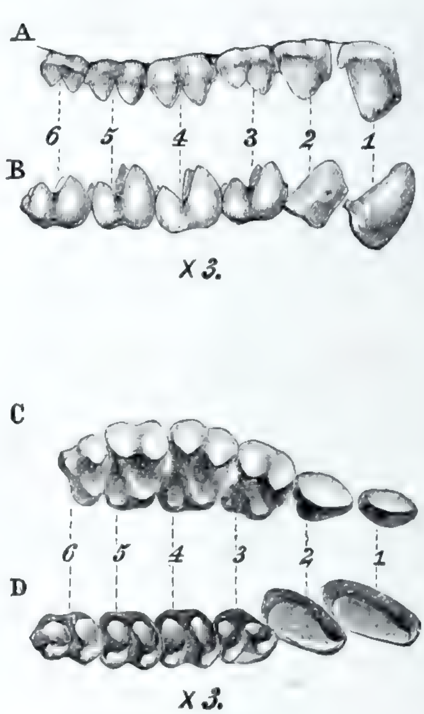

FIG. 5.
Right molars and premolars of both jaws of *Galago sennaarensis*.
A and C, upper; B and D, lower jaw.

said to be Tapiroid, the elevation which answers to the oblique ridge being shorter and less distinct, while the two transverse ridges connecting the outer and inner cusps are more obvious (fig. 5, D).

Galago maholi, also, has the inner posterior cusp of the last upper molar obsolete, and Tapiroid lower molars, the last of which is quinquecuspid.

Galago allenii has the inner posterior cusp of the third upper molar well developed; the lower molars are provided with an oblique ridge, nearly reaching the inner anterior cusp, while the third has a large fifth cusp.

In *Galago minor* the inner posterior cusp of the third upper molar is obsolete ; the oblique ridges of the lower molars are tolerably well marked, and the last has a fifth cusp.

Otolicnus garnettii and *O. crassicaudatus* have the inner posterior cusps of the third upper molars rudimentary, the oblique ridges of the lower molars but little developed, and the fifth cusp of the third lower molar rudimentary.

The upper molar teeth of the ordinary Lemurs (*Varecia*, *Lemur*, and *Prosimia*, Gray) have the inner posterior cusp obsolete, or very

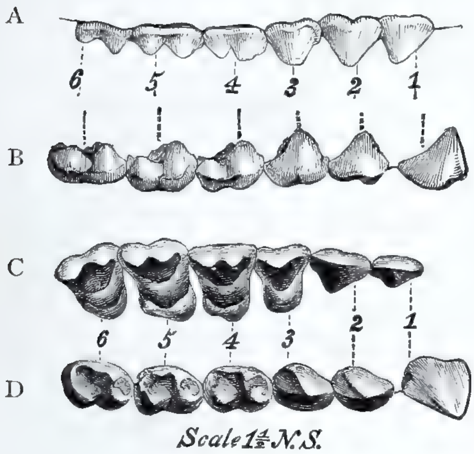

FIG. 6.
Right molars and premolars of *Lemur catta.*
A and C, upper ; B and D, lower jaw.

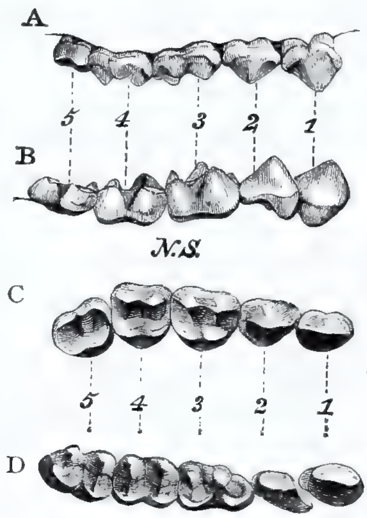

FIG. 7.
Right molars and premolars of *Lichanotus indri.*
A and C, upper ; B and D, lower jaw.

small ; and a very strongly developed cingulum, internally. The oblique ridges are sometimes present, sometimes obsolete.

The lower molars have the oblique ridge and the anterior basal process so developed as to assume, in some cases, a doubly crescentic or Rhinocerotic character (fig 6, D).

In the Indri (fig. 7), lastly, there is a type of dentition which departs still further from that of Angwántibo. Of the upper five grinders, the two anterior are unicuspidate, and like the premolars of other Lemurs ; the other three are quadricuspidate, the hindermost being the smallest. Each pair of cusps is united by a transverse ridge, and there is no oblique ridge.

In the lower jaw, also, the first and second grinders are unicuspidate, and premolar-like. The third has four cusps, connected in pairs by ridges, which are disposed obliquely from within outwards

and forwards. The anterior external cusp is continued by a curved ridge on to the margin of the large anterior basal process of the tooth; and the posterior external cusp is connected by an oblique curved ridge with the antero-internal. Thus the tooth acquires a doubly crescentic, Rhinocerotic pattern.

In the next grinder, which is also quadricuspidate, the anterior basal prolongation is reduced, and the ridges connecting the pairs of cusps are transverse to the axis of the jaw. There is no oblique curved ridge.

The last molar is like the preceding; but there is a fifth cusp, and the ridges which connect the pairs of cusps are oblique, sloping from within backwards and outwards, or in the opposite direction to that observed in the antepenultimate tooth.

There is, in both jaws, a much greater difference between the second grinder and the third, than between the third and the fourth, so that, except for the caution suggested by the similarity of the last premolar to the first molar in *Galago sennaarensis*, &c., one might suspect the third tooth to be a true molar, and consider that, in these animals, it is a premolar, and not a molar, which is suppressed.

The roof of the palate of the Angwántibo exhibits altogether nine transverse ridges, each of which is convex forwards and concave backwards. The eight anterior ones extend from a given tooth to the corresponding tooth of the opposite side. The first lies between the outer incisors, and the others between the following six grinding-teeth. There is a faint ridge behind the last molars, beyond which the soft palate continues the roof of the mouth for half an inch. In the interval between the first two ridges, in the middle line, there is a small round aperture which ends cæcally; but in front of this and of the first ridge are two small crescentic apertures, the concavities of which are turned towards one another. Into either of these a style can be passed upwards, outwards, and backwards for a considerable distance. These passages are the so-called ducts of Stenson.

Mr. Murray has noticed a similar structure in the palate of *Galago murinus* as "two small orifices (as large, however, as the root of the superior incisors) situated in the middle space between the two incisors on each side, but a little behind their line. Their position suggests an analogy to Jacobson's vesicles in the Horse; and on tracing their origin, we find that they lead to the nasal orifice, expanding before they reach it into a sort of sac, which appears to communicate, by a narrow and short canal, with the nasal orifice, in this respect differing from Jacobson's sac, which does not communicate directly with the exterior" ("Supplementary Remarks on the genus

Galago," Edinburgh New Philosophical Journal, new series, Jan, 1860). Burmeister has observed them in *Tarsius* (Beiträge, p. 103); Van der Hoeven in the Potto (Ontleedkundige Onderzoek van den Potto van Bosman, p. 47); Hoekema Kingma in *Otolicnus peli* (Eenige Vergelijkend-ontleedkundige Aanteekeningen over den Otolicnus Peli, p. 32).

The tongue, long and narrow, is marked by depressions corresponding with the palatine ridges. At its base, as in most Lemurs, are three circumvallate papillæ, arranged in a ▽, the apex of which is directed backwards. Under the tongue is the characteristically Lemurine sublingua, a broad, lyre-shaped plate, 0·35 inch long, by 0·2 inch wide at its truncated free end.[1] The under surface of this plate presents a median keel, on each side of which is a furrow. The keel ends in a sharp point in the middle of the free edge, the lateral halves of which are also serrated, each exhibiting three or four points.

The mucous membrane of the floor of the mouth, between the tongue and the mandibular rami, is raised into two sharp ridges with undulating edges; and these end in front in two pointed free processes, one on each side of the frænum.

In the Potto, Van der Hoeven (*l. c.* p. 48) describes a very similar appendage beneath the sublingua, and states that the ducts of the submaxillary and sublingual glands open on its free edge, whence he has no doubt that it answers to the caruncula linguæ. Burmeister, in *Tarsius* (*l. c.* p. 106), describes what seems to correspond to the sublingua (*mihi*) as the "Lytta," and that which appears to answer to the second appendage as "Unterzunge."

There is no uvula. The tonsils are well developed; the epiglottis projecting, and shaped like the broad end of a shoeing-horn.

The distance from the lips to the cardiac orifice of the stomach is, measured in a straight line, 5 inches.

The stomach (fig. 8) is 1½ inch long and about 1 inch in vertical diameter. The œsophagus opens on the pyloric side of the centre of its lesser curvature; the cardiac division of the stomach is consequently very large, and indeed larger than the pyloric division. At the pylorus there is no complete valve, but merely a constriction, which leaves a wide passage of communication between the stomach and the duodenum. The wall of the pyloric division is rather thicker than that of the cardiac end, in which the mucous membrane is raised into irregular longitudinal folds.

The small intestine remains of nearly the same width (about 0·4

[1] It is therefore somewhat larger in all its dimensions than in Dr. Smith's specimen.

inch) throughout; from the pylorus to its junction with the colon it is 26 inches long.

The large intestine, about 0·7 inch wide, is devoid of longitudinal muscular bands or sacculations, nor is it divided definitely into colon and rectum; it is 14 inches long.

As the gullet and oral cavity are 5 inches long, the alimentary canal is altogether $(5+1\frac{1}{2}+26+14)=46\frac{1}{2}$ inches long; or a little more than four and a half times as long as the body.

In the Potto the proportion is as 6 or 6·5 to 1; in *Stenops javanicus* 3·5 to 1; in *Stenops gracilis* 4 to 1; in *Otolicnus peli* 4·9 to 1. (See Van der Hoeven, 'Potto van Bosman,' p. 52.)

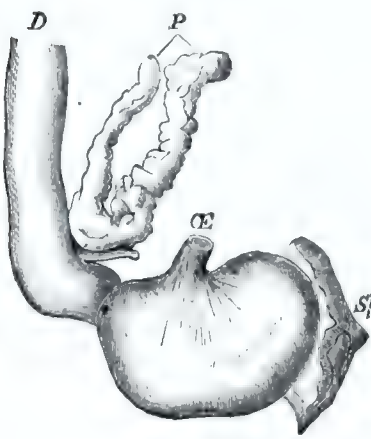

FIG. 8.

The stomach, with the œsophagus (*Œ*), the duodenum (*D*), the pancreas (*P*), and the spleen (*Sp*) of the Angwántibo. Nat. size.

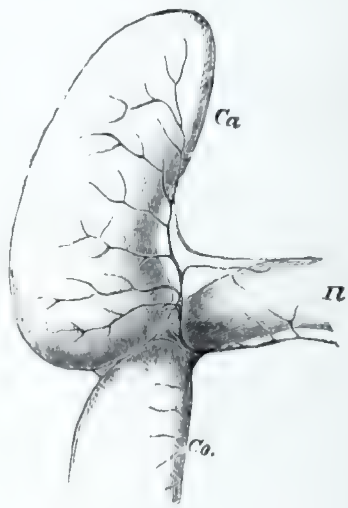

FIG. 9.

The ileum (*Il*), colon (*Co*), and cæcum (*Ca*) of the Angwántibo. Nat. size.

Where the large and small intestines join, the cæcum is given off. This is cylindroidal, somewhat curved, and $2\frac{1}{2}$ inches long by 0·9 inch in diameter. It has no vermiform appendix (fig. 9).

The liver (fig. 10) is a very irregularly shaped body, which, if spread out on a flat surface, nearly covers an area 2·2 inches wide by 1·85 inch long. It is broken up into numerous lobules by radiating fissures of greater or less width; but it may be resolved into the same components as that of Man, by taking into account the attachment of the ligaments, and the position of the vessels, gall-bladder, and ligaments.

Thus the upper surface (fig. 10, A) exhibits the attachment of the broad ligament, *m*; the moiety of the liver to the left of this (*f*, *g*, *h*)

answers to the left lobe of the Human liver, that to the right (*a*, *b*, *c*, *e*) to the right lobe in Man. But, in the Angwántibo, the left lobe is the larger and more solid, being divided by narrow fissures only into three lobules (*f*, *g*, *h*). The fissure between *f* and *g* is far deeper than the other, extending from the front margin nearly to the portal vessels.

The right half is divided by deep and wide fissures into four lobules (*a*, *b*, *c*, and *e*). The largest of these (*e*), is situated between the ductus venosus and the gall-bladder (*d*); it therefore corresponds to the lobulus quadratus. The other three are subdivisions of the right lobe. Besides these, on the under surface of the liver, behind the portal vessels, is a small lobule, which is transversely elongated,

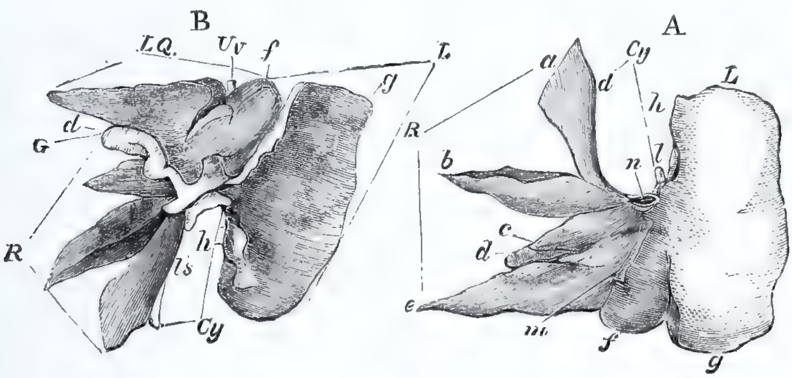

FIG. 10.

The liver of the Angwántibo. A, viewed from above; B, from below. *Cy*, coronary ligament; *LQ*, lobulus quadratus; *R*, right; *L*, left lobe; *ls*, lobulus Spigelii; *Uv*, umbilical vein; *n*, hepatic vein.

and raised into a point at each end. This corresponds with the lobulus Spigelii, and indeed somewhat resembles that part in the Orang.

The coronary ligament is attached to the edge of the hindermost division of the right lobe, and, for a short distance, to the lobule *h* of the left lobe.

The gall-bladder is long and somewhat undulating; in consequence of the great breadth of the lobulus quadratus in front, its end is turned more to the right side than forwards.

The ductus choledochus opens into the duodenum at not more than 0·4 inch from the pylorus. Fixed upon it, as it were, close to its termination, is the pancreas, which consists of two branches, one of which lies behind the stomach and nearly touches the spleen by its free end, while the other is enclosed in the loop of the duodenum (fig. 8).

The spleen (fig. 8) is 1·5 inch long and 0·3 inch wide in the middle; it is very flat, and tapers to each end. It is attached by the lesser omentum to the cardiac end of the stomach, and does not extend along its great curvature. The alimentary canal thus much resembles that of the Potto (Van der Hoeven, *l. c.* pp. 50, 51). In the latter, however, the stomach forms a small cæcal dilatation beside the pylorus, and the colon is sacculated, though the cæcum is devoid of sacculations. Neither in the Potto, nor in *Otolicnus peli*, nor in *Tarsius*, is there any appendix vermiformis, though Schroeder van der Kolk, and Vrolik find it to be represented in *Nycticebus* (Recherches d'Anat. Comp. sur le genre *Stenops*).

The liver appears to be somewhat more subdivided than in the Potto, but not more than in *Stenops* (Sch. K. & V.). The ductus choledochus opens much nearer the pylorus than in either *Tarsius* or the Potto, in which it ends in the descending part of the duodenum. The pancreas is divided into lobes in *Tarsius*, *Otolicnus*, and *Stenops* (Schroeder van der Kolk and Vrolik). The spleen is confined to the cardiac end of the stomach, not attached along its greater curvature as in *Tarsius*, the Potto, *Nycticebus*, and *Loris*.

The arterial part of the vascular system of the Angwántibo had been partially injected by Mr. Murray, with the view of determining the existence and the nature of any retia mirabilia which might exist. Mr. Murray was unfortunately prevented, however, from carrying his examination of the specimen, while freshly injected, further than the brachial artery, which, he writes, exhibited "a longitudinally striated appearance. I meant to have dissected these striations fully and delicately out, and expected to find that they were composed of a series of vessels. . . . . I reasoned that it would answer the same purpose, whether the artery was broken up into many branches spread all about the arm, or packed in one tube. . . . . . When I last looked at it the striations were much less visible than at first. At first they were wondrous distinct."

Unacquainted with these observations, I, at first, nearly failed to make out the existence of any rete mirabile in either the upper or the lower extremities. Occupying the place of the brachial and femoral vessels, I found what had all the appearance of simple trunks, filled evenly, though imperfectly, with the red injection-mass; and it was only on finding myself unable to pass a fine style into the supposed arteries, that I was led to examine their structure more minutely by the help of transverse sections and the microscope. Each trunk now turned out to be a dense and firm cord of connective tissue, traversed longitudinally by multitudinous trunks, some of

which presented the remains of the red injection, while the others were empty. The former and the latter occupied opposite halves of the cord, and were not intermingled. In the femoral cord, the injected trunks were one comparatively large artery, $\frac{1}{60}$th of an inch in diameter, with strong walls, and about eighteen smaller ramuscules of between a half and a third the diameter of the large one. The un-injected trunks were of a similar size.

In the brachial cord there was a precisely similar arrangement; but the small branches were rather more numerous.

I am not aware that any rete mirabile has yet been observed having the arrangement just described; and it would be a matter of much interest to work out the details of the angeiology of this animal in a specimen better fitted for investigation.

The kidneys (fig. 11, *K*) are situated in the lumbar region, immediately below the diaphragm, the right being higher than the left by half its length. Each kidney is 0·7 in. long by 0·35 in. wide, and is shaped much like that of Man. In vertical and longitudinal section it exhibits but a single papilla. The ureters open into the bladder about half an inch above its urethral aperture, and 2 inches from its summit. The bladder is, thus, in its empty and flaccid condition about 2·5 inches long.

The suprarenal bodies (SR) are oval, 0·4 inch long, and are attached to the front and upper faces of the kidneys.

The testes (fig. 11, T) are large for the size of the animal, each being 0·7 inch long by 0·4 inch wide, without the epididymis, which is proportionately developed. The inguinal canal is open, so that a blowpipe can be passed into it and the peritoneal sac inflated. The thick vasa deferentia pass through it, and then curving over the obliterated hypogastric arteries (which can be traced up to the summit of the bladder), they bend down behind the bladder and become closely connected together. They terminate in the urethra by two apertures placed close together, upon the end and rather the under surface of a papilla-like colliculus seminalis, which is slightly bifid at its extremity (fig. 12, B).

At first I took the notch which causes this appearance for the mouth of an uterus masculinus, which I imagined might lie on the elevated ridge which extends between the apertures of the vasa deferentia and those of the ureters; but careful examination did not reveal the existence of any such structure. Two longitudinal folds of mucous membrane, along which the apertures of the prostatic ducts (*Pr'*, fig. 12, B) are situated, extend from the colliculus and form the lateral boundaries of a wide fossa, which it overhangs. This fossa receives at its upper and back part, by two separate apertures.

the ducts of two large oval sacs, which are perfectly distinct from one another, though their inner walls are united for some distance. The walls of these sacs are raised into oblique folds, and they lie at the back of the neck of the bladder behind the vasa deferentia, and occupy the place of the vesiculæ seminales. As they do not com-

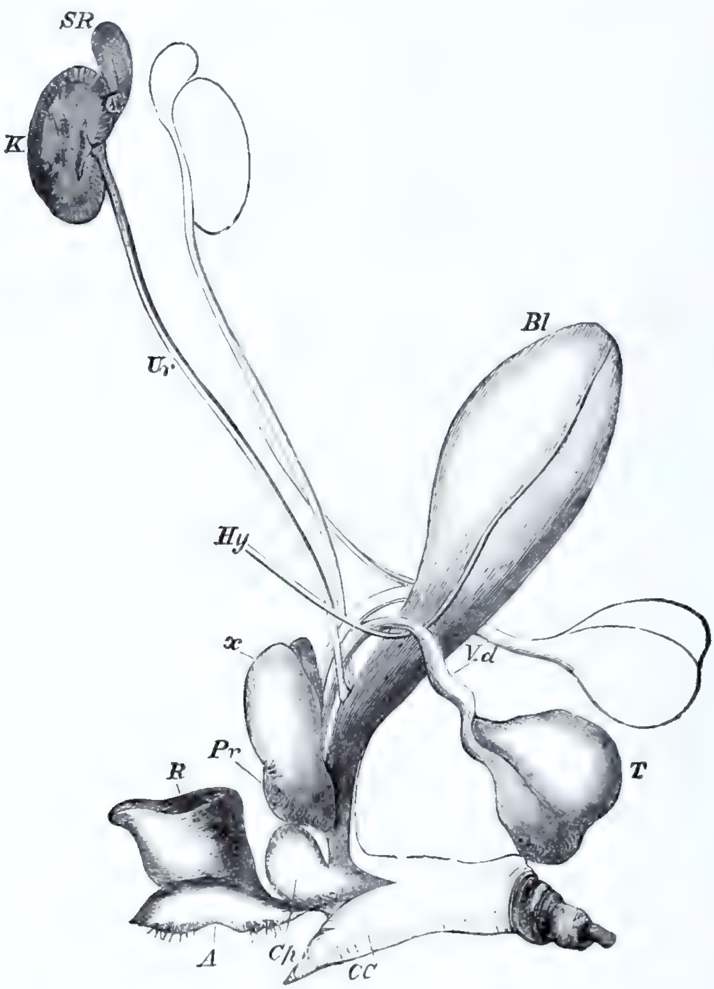

Fig. 11.

The uropoietic and male reproductive organs of the Angwántibo (nat. size). *A*, anus; *R*, rectum; *K*, kidney; *SR*, suprarenal bodies; *Ur*, ureter; *Bl*, bladder; *Hy*, hypogastric artery; *T*, testis; *V.d*, vas deferens; *Pr*, prostate; *Cp*, Cowper's glands; *CC*, corpora cavernosa.

municate directly with the vasa deferentia, however, I am doubtful whether they ought to be considered as representing the vesiculæ seminales, or as a large uterus masculinus.

These sacs are distinguished externally from the prostate (*Pr*) only by a slight constriction; but their ducts pass in front of that gland, which lies altogether at the back of the urethra, so that the front wall of the latter is free and uncovered by the prostate. The

prostate is pyriform, broad above, narrow below, and has the ordinary structure.

A "membranous portion" of the urethra unites the prostatic part with the slightly dilated bulbous portion and its continuation lodged in the corpus spongiosum. The bulb receives the ducts of the two large oval Cowper's glands (*Cp*, figs. 11, 12), each of which has thick walls and a central cavity continuous with the ducts.

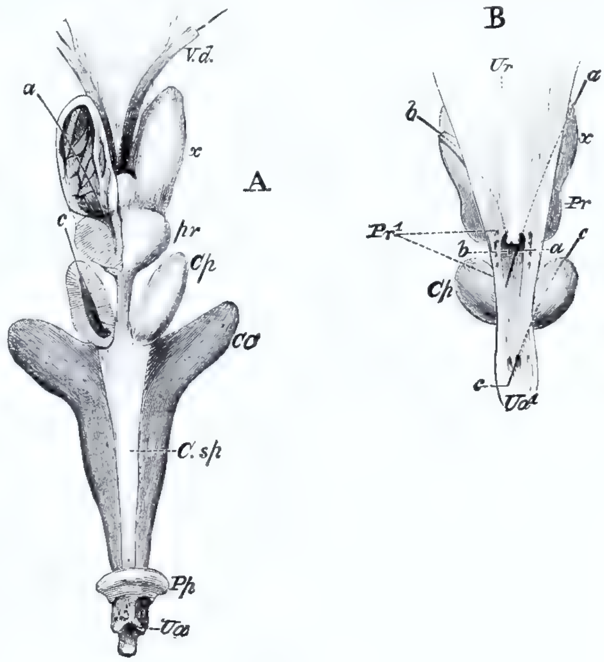

FIG. 12.

The vasa deferentia, accessory generative glands and penis of the Angwántibo, dissected, and drawn of twice the natural size. A, viewed from behind; B, from in front, and slit open; *a*, *b*, *c*, bristles introduced into the oval sac, vasa deferentia, and Cowper's glands, respectively. In A: *C. sp*, the corpus spongiosum; *Pp*, the prepuce; *Ua*, the urethral aperture. In B: *Ur*, the apertures of the ureters; *Pr'*, of the prostate ducts; *Ua'*, the urethral canal.

The os penis, 0·75 inch long, is situated between the corpora cavernosa, extending from the apex of the penis backwards in the middle line.

The glans penis consists of a median, curved, subcylindrical portion supported by the extremity of the bone of the penis, and of a sort of hood, bifid below, which surrounds the base of this. The hood has a tuberculated surface; and the urethra opens between the lobes formed by its inferior bifurcation, and therefore at some distance behind the apex of the organ.

According to Van der Hoeven's account (*l. c.* p. 54), the male reproductive organs of the Potto must be very similar to those of the Angwántibo; and Kingma's description and figures demonstrate the like for *Otolicnus peli*. Kingma, in fact, has worked out the anatomy of the parts more thoroughly than Van der Hoeven; for he shows that, as in the Angwántibo, the hollow vesicles connected with the prostate open independently of it and of the vasa deferentia, and does not admit them to be vesiculæ seminales. But it is unsafe to come to a conclusion respecting the nature of these parts without some knowledge of their development.

In his recently published "Revision of the Species of Lemuroid Animals" (Proc. Zool. Soc. 1863, p. 129), Dr. J. E. Gray has separated the Angwántibo from *Perodicticus*, and has made it the type of a new genus, *Arctocebus*. The genera *Perodicticus* and *Arctocebus* are differentiated as follows (*l. c.* p. 150):—

"++ *The hand broad; the index finger abortive, clawless; eyes moderate.* Perodicticina.

"15. PERODICTICUS, Bennett.

"Tail shorter than the body. The hands and feet large. Fingers and toes free at the ends; the index finger rudimentary, but distinct. Lower cutting teeth large and prominent, and projecting. The apices of the vertebræ of the back, neck, and withers projecting beyond the skin, like prickles.

"16. ARCTOCEBUS.

"Tail very short. Hands and feet small, with the lower phalanges (not including the thumb) united in the skin, the two upper joints free; the index finger abortive, reduced to a tubercle. Lower cutting teeth small, hyaline, hidden by the lips."

Leaving the skeleton (the characters of which I propose to discuss on a future occasion) out of consideration, the facts which I have brought forward in the present communication appear to me to justify, though on grounds different from those stated by Dr. Gray, the establishment of the new genus *Arctocebus* for the Angwántibo. This genus is distinguished from all other *Lemuridæ* by the combination of the following characters:—

The tail rudimentary. The pinna of the ear has two projecting shelf-like lamellæ above the auditory meatus. The index finger is rudimentary and nailless. The dental formula—$i. \frac{2-2}{2-2}$; $c. \frac{1-1}{1-1}$; $pm. \frac{3-3}{3-3}$; $m. \frac{3-3}{3-3}$. The anterior upper molars have oblique ridges and are quadricuspid, the last is tricuspid. The last lower molar quinquecuspid.

In *Perodicticus*, on the other hand, the tail is distinct, though short. The pinna of the ear has only one complete shelf-like lamella. The index finger is rudimentary and nailless. The dental formula is—$i. \frac{2-2}{2-2}$; $c. \frac{1-1}{1-1}$; $pm. \frac{3-3}{3-3}$; $m. \frac{3-3}{3-3}$. The anterior upper molars have oblique ridges and are quadricuspid, the last is bicuspid. The last lower molar is without a fifth cusp.

END OF VOL. II